The winter movements of Weddell seals in the sea ice zone of eastern Antarctica

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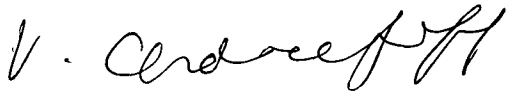
July 2010

Declaration of originality

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma in any tertiary institution, and that, to the best of my knowledge and belief, the thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.



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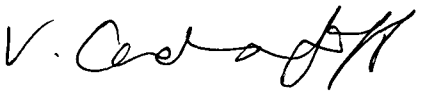

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Abstract

Winter sea ice plays a major role in the Antarctic ecosystem due to its influence on the abundance and recruitment of keystone species and the secondary production associated with the ice edge on which many Antarctic predators rely. For one of these predators, the Weddell seal, long term data sets indicate that the population dynamics of this species is closely tied up with the winter ice environment. However, very little information exists on the winter movements of Weddell seals or their interactions with the winter ice environment. Over 3 years, adult female Weddell seals were equipped with satellite relay data loggers at Dumont d'Urville and the Vestfold Hills to determine winter behaviour and the role of the local environment, including ice concentration and weather, on this behaviour.

Satellite relay data loggers transmit information via the Argos satellite system on seal location and behaviour. However, the ability to answer spatial questions of this data and the role of the environment in animal movement is hampered by aspects of the animal's behaviour and Argos location error. For Weddell seals, it was found that haulout locations were over represented in the data set. As such, any spatial analyses that include haulout locations of Weddell seals run the risk of overestimating the importance of haulout sites. In addition, when extracting environmental information at highly uncertain Argos locations, there is a high probability of extracting the wrong information leading to inaccurate assessments of the role of the environment in animal behaviour. A state-space modelling approach was applied to the Weddell seal tracks to address this. The resulting locations were a vast improvement on Argos locations when compared to GPS tracks of the same individuals and haulout locations were fixed to avoid over estimation of their importance. The error distribution associated with each location was incorporated into an approach whereby the extraction of a location specific

environmental variable was weighted by the location's error distribution. This method of extracting environmental variables was then applied to assess the role of the local environment on the winter behaviour of Weddell seals.

The local environment influenced both winter haulout and foraging behaviour with Weddell seals tending to haulout more under conditions of low wind speed and higher temperatures and remain submerged when the opposite was true. Seals were also more likely to terminate diving bouts under conditions of very heavy ice concentration when compared to lighter ice concentrations in the fast ice environment. Whilst winter foraging could be classed as either predominantly benthic or pelagic with a high level of individual variability, all Weddell seals employed both foraging strategies at some stage throughout the tracking period.

These results reveal that aspects of the local environment have the ability to drive the winter behaviour of Weddell seals and must be considered in conjunction with the influence of prey availability and larger scale climatic phenomena. Individual foraging strategies imply that Weddell seals within the one population may display varied responses to climate-mediated changes in prey availability. As such, Weddell seals are vulnerable to changes in the ice environment that are long term and large scale as well as short term and local.

Statement of publication and co-authorship

Publications produced as part of this thesis

Chapter 2 contains material published as:
Andrews-Goff V, Hindell MA, Field IC, Wheatley KE, Charrassin JB, 2010. Factors influencing the haulout behaviour of Weddell seals: consequences for satellite telemetry. Endangered Species Research 10: 83 – 92

The following people and institutions contributed to the publication of the research undertaken as part of this thesis:

Virginia Andrews-Goff (University of Tasmania; 60% contribution) was responsible for fieldwork, data analysis, interpretation of results and manuscript preparation.

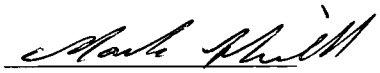
Mark A Hindell (University of Tasmania; 20% contribution) provided guidance, supervision and assisted with fieldwork relating to all aspects of the PhD and producing publishable manuscripts.

Jean-Benoit Charrassin (Museum of Natural History, Paris; 10% contribution) provided guidance, supervision and assisted with fieldwork relating to all aspects of the PhD and producing publishable manuscripts.

Iain Field (Macquarie University; 5% contribution) assisted with fieldwork.

Kathryn Wheatley (Deakin University; 5% contribution) assisted with fieldwork.

We the undersigned agree with the above stated "proportion of work undertaken" for each of the above published (or submitted) peer-reviewed manuscripts contributing to this thesis:

Signed: 

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Intent to submit publications produced as part of this thesis

Chapter 3 contains material that will be submitted as:
Andrews-Goff V, Hindell MA, Patterson TA, Field IC, Wheatley KE, Charrassin JB. Weddell seal movements in the winter ice environment: incorporating a state space approach to account for uncertainty when extracting location-specific environmental variables.

Chapter 4 contains material that will be submitted as:
Andrews-Goff V, Hindell MA, Patterson TA, Field IC, Wheatley KE, Charrassin JB. Winter foraging strategies of Weddell seals – individual variability and the influence of local environmental conditions.

The following people and institutions contributed to the publication of the research yet to be submitted, undertaken as part of this thesis:

Virginia Andrews-Goff (University of Tasmania; 60% contribution) was responsible for fieldwork, data analysis, interpretation of results and manuscript preparation.

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Toby A Patterson (Commonwealth Industrial and Scientific Research Association (CSIRO) Marine and Atmospheric Research; 15% contribution) developed the Kalman filter used to smooth Weddell seal tracks

Iain Field (Macquarie University; 2.5% contribution) assisted with fieldwork.

Kathryn Wheatley (Deakin University; 2.5% contribution) assisted with fieldwork.

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Acknowledgements

As I compete my PhD, I cannot help but be amazed by the experiences along the way. I have been lucky enough to carry out fieldwork in the most incredible location on earth and have had the privilege to work on one of the most relaxed yet most extreme animals on earth. Couple this with the opportunity to live in Paris to fulfil requirements of my cotutelle arrangement with the Museum of Natural History and what more could I ask for?

These opportunities would not have been possible without the support of both the French and Australian Antarctic programs under the approval of the University of Tasmania Animal Ethics Committee (permit A8523). Fieldwork at Dumont d'Urville was made possible through the support of Charly Bost and Christophe Guinet (CNRS) mediated through Jean-Benoit Charrassin. On the Australian side was the hard work of both Iain Field and Kathryn Wheatley supported logistically by the Australian Antarctic Division (AAS project 2794). Financial support through a Tasmanian Graduate Research Scholarship provided to me by the University of Tasmania was simply invaluable.

I cannot emphasise enough the ability of my Australian supervisor, Mark Hindell to guide me in the right direction. A mere thank you for your insight, encouragement, patience and persistence plus your support and feedback in the final stages of thesis writing is barely adequate. Regardless, thank you so much.

To my French supervisor Jean-Benoit Charrassin, the adventure that has been my PhD is mostly due to you. Your support and encouragement has lead me from Antarctica to Paris to California to Buenos Aires and once again a huge thank you is warranted. JB, Alexia and Mayeul – thank you for welcoming me into your lives in

Paris, providing me with an amazing work place at the Museum of Natural History, teaching, feeding and immersing me in all things French.

To all the hard little workers in the field too numerous to mention, thank you so much for your help. To all those on station who made me feel so welcome, thank you. To the French chefs on station – thank you… I think.

To everyone in the Marine Predator Unit, your friendship, support, coffee breaks and Friday afternoon drinks have kept me sane. Thank you for just being there. To Toby Patterson whose Kalman filter is key to this work, thank you so much for persisting with me through such a hectic schedule, marriage and a baby.

To my long suffering partner Brent, who has waved goodbye to me on so many occasions, who has spent his summer holidays without a surf buddy and who has had to deal with the stressed out me more often than not lately, I am eternally grateful. Your support, encouragement, optimism and the fact you stuck with me have amazed me throughout these last few years and I most definitely could not have done it without you.

Finally, to my mother and her ability to mark every milestone PhD moment with a bottle of champagne, a card or by imparting an amazing sense of achievement - thank you for believing in me.

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1. Introduction

The importance of the Antarctic winter sea ice environment

Antarctic sea ice plays a critical and highly dynamic role in the global climate system and the ecology of the Southern Ocean through its extent, structure and seasonality (Massom and Stammerjohn 2010). The annual formation of sea ice is the basis of current movements globally and plays a key role in the formation of bottom water contributing to the upwelling of nutrients and thermohaline circulation of continental shelves and the deep ocean (Moline *et al.* 2008).

When winter sea ice melts in spring, it creates a stable, low salinity surface layer that can affect primary productivity (Moline *et al.* 2008), generating extensive phytoplankton blooms (Smith and Comiso 2008) and attracting intense feeding by higher trophic level organisms (Arrigo and Thomas 2004). Antarctic krill *Euphausia superba*, a keystone species in the Southern Ocean and an important prey source for higher predators directly and indirectly, are inextricably linked to the dynamics of the sea ice environment by the nature of their life cycle (Quetin *et al.* 2007). In the western Antarctic Peninsula region, winter sea ice plays a role in krill recruitment and abundance (Loeb *et al.* 1997) whilst in east Antarctica, more krill are observed with more sea ice (Nicol *et al.* 2000). Sea ice is also a crucial food source of algae for grazing species such as Antarctic krill (Quetin and Ross 1991). A crucial trophic link and important food source for Antarctic predators, the pelagic Antarctic silverfish *Pleuragramma antarcticum*, relies on sea ice both to spawn and as an early nursery (Moline *et al.* 2008). For seabirds and marine mammals, sea ice also plays a structural role by providing a platform for resting and reproduction (Eicken 1992).

Winter sea ice extent and volume is predicted to decline by 24% and 34% respectively by the year 2100 (Arzel *et al.* 2006). Recent and major regional changes in sea ice cover have had dramatic impacts on the structure and dynamics of the Antarctic ecosystem where animals at all trophic levels are adapted not only to its presence but also its seasonal rhythms and properties (Massom and Stammerjohn 2010). The impact of changes in winter sea ice on top predators is varied according to life history and foraging ecology. For example, the population of Adélie penguins in the western Antarctic Peninsula is declining due to a gradual decrease in the availability of winter sea ice (McClintock *et al.* 2008). This is partly due to the foraging ecology of Adélie penguins. During the winter, Adélie penguins forage in areas where the topography of the sea floor creates upwellings from the circumpolar current around which krill and fish congregate. Adélie penguins only forage during the day, so to access and remain close to these spots, Adélie penguins migrate over winter sea ice. Adélie penguins therefore lose access to the most productive winter foraging regions as winter sea ice extent decreases. The population decline is also partly due to the life history of Adélie penguins. With the loss of sea ice one factor causing a change in weather patterns due to higher levels of evaporation and cloud cover related to the exposure of open ocean, the number and severity of spring blizzards during the breeding season has increased. When the snow melts from these storms, nests are flooded, eggs fail and chicks are killed. In contrast, chinstrap and gentoo penguins that have established only relatively recently in the western Antarctic Peninsula are prospering. By maintaining their sub-Antarctic breeding chronology and breeding approximately three weeks later than Adélie penguins, they reduce the risk of nest flooding in the aftermath of spring blizzards. Both species also forage in ice-free areas with chinstrap penguins migrating north beyond the

sea ice zone whilst gentoo penguins maintain colonies close to areas where fast currents or upwelling ensure that sea ice does not persist.

Another Antarctic predator, the Weddell seal is influenced by winter sea ice both due to its foraging ecology and life history, but for a different suite of reasons. Weddell seals breed on fast ice, which if too thick or persistent in the austral spring can lead to the closure of predictable annual ice cracks. The consequence of the B - 15 iceberg trapping fast ice in McMurdo Sound was fewer adults arriving at breeding sites and fewer pups being born (Siniff *et al.* 2008). Weddell seals are also influenced by El Niño – Southern Oscillation, through variation in ice concentration and extent (Testa *et al.* 1991) that may influence prey availability, impacting on the foraging success of pregnant females (Hadley *et al.* 2007a). In particular, winters of extensive ice result in increased adult female survival (Hadley *et al.* 2006) and a higher probability of a female giving birth to its first pup in the spring (Hadley *et al.* 2007b). On the other hand, summers of extensive sea ice result in decreased foraging success of pregnant females (Proffitt *et al.* 2007).

The majority of studies over the last five decades focus on the ecology of the Weddell seal throughout the austral spring and summer, when there are increased numbers of Weddell seals hauled out for pupping and moulting (Kooyman 1968). Early anecdotal accounts suggest that Weddell seals remain in local waters throughout the year (Wilson 1907; Lindsey 1937; Sapin-Jaloustre 1952). Other studies indicate seasonal northward and southward movements during the winter related to fast ice (Kooyman 1968). More recently, Testa (1994) found that Weddell seals remained within 50 - 100km of their summer breeding colonies and utilised both the fast ice and pack ice environment during winter. Lake et al. (2005b) state that during winter, Weddell seals forage offshore and return to the fast-ice environment to rest. These

varying views on the movements of Weddell seals throughout the winter period may reflect behavioural differences between locations, however they highlight the need for more information on the interactions between Weddell seals and their winter sea ice environment that is so crucial to foraging success, survival and population dynamics.

Analysing animal movements: bio-logging and Weddell seals

With continued technological advancement comes the ability to better describe the winter ecology of Weddell seals through biologging, the use of miniaturized animal-attached tags for logging and/or relaying data about an animal's movements, behaviour, physiology, and/or environment (Rutz and Hays 2009). These advances include tag miniaturization, novel attachment techniques, the ability to collect behavioural and environmental information (Hart and Hyrenbach 2010), improved battery life and memory capacity (Rutz and Hays 2009). It is therefore possible to deploy tags on Weddell seals that remain attached and transmitting throughout the entire austral autumn and winter. Tags can collect information on seal movement and behaviour (*i.e.* location and dive depth) and concurrently collect information on the water column in which the seal forages (*i.e.* temperature and conductivity).

Biologging tags provide considerable insight into animal movement patterns (Rutz and Hays 2009), knowledge which is key to understanding an animal's ecology, life history, behaviour and is essential to their conservation (Rubenstein and Hobson 2004). Biologging tags commonly utilise the Argos satellite system to track the movements of free-ranging animals (Vincent *et al.* 2002). However, for many marine organisms, a high proportion of locations are of low quality with little information on the degree of measurement error (Costa *et al.* 2010) which can range from less than 150m to greater than 1000m or may simply be unknown (Service Argos – 2010). This spatial uncertainty poses a serious challenge, as it influences the ability to differentiate

between biological variability and artificial noise (Jonsen *et al.* 2005). As a result, the approach to analysing animal movement is often broken into three stages: i) error correction through pre-processing techniques, such as filtering of low quality locations to address the error associated with each Argos location, ii) calculation of movement metrics such as swimming speed and bearing from corrected paths and iii) pattern identification or statistical analysis based on these metrics to relate movement to the biology of the animal (Patterson *et al.* 2008).

Recent techniques of analysing animal movement patterns, such as state space models, are revolutionising our understanding of top predator ecology (Bograd *et al.* 2010). The state space modelling approach couples a 'process model' (a hypothetical mechanistic model of individual movement) to an 'observation model' (the probability of obtaining an observation conditional on an animal's true position or 'state') (Patterson *et al.* 2008). The state space model is therefore a time series model that predicts the future state of an animal given its current state (process model) and then weights these predictions by the likelihood of the data (observation model). In this way, the state space modelling approach integrates the three analytical stages: i) error correction, ii) calculation of metrics and iii) analysis. Location uncertainties are therefore accounted for when analysing the data set due to the inclusion of the observation model which eliminates the need to remove low quality locations in the 'pre-processing' or error correction stage.

Argos locations derived for Weddell seals, like all marine organisms, will be dominated by locations with no declared error estimate (Vincent *et al.* 2002). For example, 89% of all Argos locations detailing a northern elephant seal track had no declared error estimate (Costa *et al.* 2010). Application of the state space modelling process to Weddell seal locations therefore must take into account Argos location error

using estimates from published data such as Vincent et al. (2002). Outside of the breeding season in the austral spring and winter, Weddell seals use multiple haulout locations (Lake *et al.* 2005b). A haulout precludes the possibility of foraging therefore these locations are not informative of foraging areas. Weddell seal movement can therefore be related to phases of foraging throughout which occur non-foraging locations. These foraging and non-foraging locations need to be accounted for in the state space modelling approach when analysing Weddell seal movements to ensure that the importance of haulout locations is not over estimated. The state space model must be informed that at times when the seal is hauled out, the location generated by the model is fixed until the seal is deemed to be at sea again. If haulouts are not accounted for, the state space model will give an inaccurate view of Weddell seal movements and identification of areas important to foraging.

Individual movement patterns are complex processes shaped by life history, physiology, behaviour and habitat (Patterson *et al.* 2008). The relationship between an animal and its habitat has a direct influence on its ability to survive and reproduce through habitat mediated foraging success or the physiological constraints that a habitat may incur (Patterson *et al.* 2009), such as the timing and availability of resources (Peck *et al.* 2006). Many studies use state space models to describe animal movement (Jonsen *et al.* 2007; Bailey *et al.* 2009; Patterson *et al.* 2010) and many studies investigate the role of the environment on animal behaviour through extraction of environmental variables at an animal's location (McConnell *et al.* 1992; Guinet *et al.* 2001; Lea and Dubroca 2003). However, few studies incorporate location uncertainty when examining the relationship between animal movement and behaviour with the environment (Eckert *et al.* 2008; Patterson *et al.* 2009). Given that state space models produce an improved animal track relative to Argos with a measure of error around each location, they are

ideal to investigate animal-environment relationships that take into account location uncertainty when examining location-specific environmental covariates.

The Weddell seal

The first comprehensive description of the Weddell seal, *Leptonychotes weddelli*, was in 1907 and written by junior doctor and zoologist Edward Wilson, a member of Robert Falcon Scott's British National Antarctic Expedition -1901-1904 (Wilson 1907). This was followed 30 years later by a comprehensive description of the Weddell seal in the Bay of Wales (Lindsey 1937) followed closely by a description of the Weddell seal in Graham Land, Antarctic Peninsula (Bertram 1940). These three reports laid the foundation for further work and research published over the last five decades have made the Weddell seal one of the most studied Antarctic predators throughout the austral spring and summer. This research includes, but is not limited to, a comprehensive body of work on population dynamics (Stirling 1967; Siniff *et al.* 1977; Testa 1987; Cameron and Siniff 2004; Hadley *et al.* 2007a; Harcourt *et al.* 2007), diet (Dearborn 1965; Calhaem and Christoffel 1969; Green and Burton 1987; Burns *et al.* 1998; Lake *et al.* 2003), vocalisation (Schevill and Watkins 1965; Green and Burton 1988; Morrice *et al.* 1994; Abgrall *et al.* 2003) and diving behaviour and physiology (Kooyman 1965; Kooyman 1975; Kooyman 1981; Burns 1999; Hindell *et al.* 2002; Sato *et al.* 2003a; Wheatley *et al.* 2006b).

Amongst this large body of work, research covering behaviour and movements of Weddell seals throughout the austral autumn and winter is lacking. A study of the White Island population in the austral winter of 1981 detailed dive behaviour and used hydrophone recordings to establish winter residency (Davis *et al.* 1982). The seasonal diving behaviour of Weddell seal populations at White Island, McMurdo Sound and Terra Nova Bay were detailed in a monograph which included the winter of 1981

(Castellini *et al.* 1992). Satellite telemetry was used to study Weddell seal movements throughout the austral winter in 1990 and 1991 and revealed that the McMurdo Sound population used both fast ice and pack ice habitat throughout the winter (Testa 1994). Another satellite telemetry study which tracked the Vestfold Hills population over the austral winter of 1999 suggested that Weddell seals forage offshore and return to fast ice haulout sites to rest (Lake *et al.* 2005a). These studies detailing over-winter movement and behaviour present contrasting views on the winter ecology of Weddell seals yet there has been no subsequent research to help elucidate the role of Weddell seals in the winter sea ice environment.

Weddell seals have a circumpolar distribution, occurring in sub Antarctic and Antarctic regions and closely associated with the fast ice of the Antarctic continent and sub Antarctic islands (Lugg 1966; Croxall and Hiby 1983; Siniff 1991). Outside of the breeding season, Weddell seals have also been observed in pack ice (Stirling 1969c; Testa 1994; Stewart *et al.* 2003) in small numbers. Weddell seals are long-lived with a life expectancy of up to 27 years for females and 24 years for males (Cameron and Siniff 2004). Both male and female adult Weddell seals exhibit site fidelity by returning to their traditional breeding colonies each spring (Cameron *et al.* 2007). Pregnant females return to these haulout sites, often along predictable annual tide cracks, to pup in late October and November (Siniff 1991). In northern ranges pupping can be as early as September. Males maintain underwater territories at these haulout sites and after the five to six week pup dependency period, will mate with females underwater (Siniff 1991).

Adult Weddell seal diet varies with location and season and is diverse consisting of both benthic and pelagic species (Casaux *et al.* 2006). Generally pelagic Antarctic icefish *Pleuragramma antarcticum* are considered to make up the bulk of Weddell seal

diet (Dearborn 1965; Plötz 1986; Casaux *et al.* 1997; Burns *et al.* 1998). Antarctic toothfish *Dissostichus mawsoni* may also be an important component of adult Weddell seal diet (Calhaem and Christoffel 1969; Ponganis and Stockard 2007; Ainley and Siniff 2009). Even within one site, Weddell seal diet can vary considerably. In the southern fjords of the Vestfold Hills, Weddell seals forage benthically on *Trematomus bernacchii* and benthic prawns (Lake *et al.* 2003). Then, throughout the spring in Long fjord, they feed on the epipelagic *Pleuragramma antarcticum.* Weddell seal diet also varies temporally with the squid species *Psychroteuthis glacialis* being an important component of the diet of Weddell seals along the Mawson coast in spring (Lake *et al.* 2003). Along both the Mawson coast and the Vestfold Hills, Weddell seals also target mysid swarms indicating that they have the potential to forage with other oceanic predators in krill swarms present at the southern boundary of the Antarctic Circumpolar Current (Lake *et al.* 2003). With such a flexible foraging response, Weddell seals may minimise the influence of the dynamics of prey availability on their own population dynamics (Murdoch *et al.* 2002). For example, in the year 2000, Adélie and chinstrap penguins at Signy Island experienced a decline in reproductive success related to the dynamics of their primary prey, Antarctic krill (Lynnes *et al.* 2004). This decline was related to a reduction in prey availability due to the fact that recruitment of small krill into the population had been lacking since 1996. If these species had flexible foraging strategies, they may have been able to compensate for the low availability of krill by consuming alternative prey such as *Pleuragramma antarcticum.*

The global Weddell seal population size is approximately 800,000 (Erickson and Hanson 1990) and is essentially stable with the exception of populations close to some Antarctic bases that were harvested for dog meat (Siniff 1991). However, Weddell seals are predicted to be influenced by any environmental change that alters the sea ice

environment (Siniff *et al.* 2008). Increases in thickness of near-shore ice will impact the ability to access traditional breeding areas, changes in the persistence and thickness of sea ice will lead to a loss of area suitable for breeding and these same changes in persistence will influence prey availability and therefore foraging success of Weddell seals.

Aims and thesis outline

Weddell seals are influenced by both broad scale (*i.e.* El Niño – Southern Oscillation (Testa *et al.* 1991)) and small scale climatological events (*i.e.* local weather (Lake *et al.* 1991)), are sensitive to changes in the winter ice environment (Siniff *et al.* 2008) yet very few studies have examined their winter behaviour and movements or their interactions with the winter ice environment. As such, the aim of this research is to examine how Weddell seals interact with the winter ice environment, especially considering the predicted changes in winter sea ice structure and extent (Massom and Stammerjohn 2010). Specifically, this research aims to gain an understanding of Weddell seal winter movements and behaviour in two Antarctic locations – the Vestfold Hills (68° 33′ S, 78° 15′ E) and Dumont d'Urville (66° 40′ S, 140° 00′ E). Data from satellite relay data loggers that provide information on location and diving behaviour are used to:

1. Quantify winter haulout, the influence of the local environment on winter haulout and the consequence of winter haulout behaviour to satellite telemetry.
2. Measure the location error in the Weddell seal tracking data set by applying a state space modelling approach employing a Kalman filter and then develop a method accounting for this location error when extracting location specific environmental data.

3. Quantify winter diving behaviour by identifying foraging strategies, habitat use and determining the influence of the local environment on diving behaviour.
4. Incorporate Weddell seal winter behaviour into an assessment of the sensitivity of Weddell seals to climate change.

An outline of each chapter is presented below:

Chapter 2: Winter haulout behaviour and the consequences of winter haulout behaviour on satellite telemetry

This chapter describes the winter haulout behaviour of Weddell seals in terms of timing and monthly patterns. Haulout behaviour is then modelled using local environmental variables to determine if weather and ice conditions play a role in haulout. Given that periods of haulout are ideal times for successful satellite uplinks (and conversely less time is spent on the surface while foraging and so uplinks are less common, perhaps resulting in an under representation in the location record), the uplink rate at sea and at haulout is compared and then discussed in terms of the consequences to spatial interpretation of animal movements. The results provide insight into the diel and nocturnal nature of haulout during winter. The influence of the local environment on haulout behaviour is discussed in relation to thermoregulatory requirements. The tendency of haulout locations to be over represented in the data set is highlighted and recommendations are made for how best to avoid the importance of haulout sites being overestimated in movement analyses of ice seals in general.

Chapter 3: Addressing Argos location error of Weddell seals moving throughout the winter ice environment

This chapter details the application of a state space modelling approach employing a Kalman filter to correct Argos location error and compares the Kalman smoothed tracks to Global Positioning System (GPS) tracks of the same individuals. A new method is developed that incorporates location uncertainty when extracting location specific environmental information and is applied to the movements of Weddell seals in the winter ice environment. This method, that weights ice concentration according to the error distribution of each Kalman smoothed location, is one of the first attempts to incorporate location uncertainty when relating animal movement to the environment. The results indicate that both the Kalman filter and the weighted mean approach are successful when applied to Weddell seal tracking data and are ideal for analysing historic Argos data sets predating GPS.

Chapter 4: Winter diving behaviour of Weddell seals and the role of local environmental variables in diving bout behaviour

This chapter quantifies the diving behaviour of Weddell seals throughout the austral autumn and winter with the aim of identifying individual foraging strategies, the influence of bathymetry and the influence of local environmental variables on these strategies. The tendency for haulout locations to be over-represented in the Weddell seal tracking data, as suggested in Chapter 2, and Argos error are addressed with the Kalman filter state space modelling approach presented in Chapter 3. All environmental variables are extracted using the weighted mean approach in Chapter 3. The results provide insights into the individual variability associated with foraging strategies and the very local nature of foraging for all individuals tracked. The influence of the local

environment on diving bout behaviour is discussed in relation to thermoregulation and survival.

Chapter 5: General discussion

In this final chapter, the results of the three research chapters are discussed while incorporating them into an assessment of the sensitivity of Weddell seals to climate change. The sensitivity matrix includes information on population size and range, habitat and diet specificity, habitat feature reliance and potential for population growth. This discussion results in firm conclusions on the future of Weddell seals in the face of a changing climate and compares Weddell seal sensitivity to the sensitivity derived for Arctic marine mammals.

The thesis is structured so that chapters 2 – 4 are intended to be independent scientific articles that have either already been published or are a manuscript in preparation for publishing. Virginia Andrews-Goff was senior author for each chapter and responsible for collection of data, data analysis, interpretation and manuscript preparation. However, co-authors contributed to the facilitation of the project, collection of data, data analysis and preparation of the manuscripts. These co-authors are listed at the start of each chapter and in the statement of publication and co-authorship.

2. Factors influencing the winter haul out behaviour of Weddell seals: consequences for satellite telemetry.

Published as: Andrews-Goff V, Hindell MA, Field IC, Wheatley KE, Charrassin JB, 2010. Factors influencing the winter haulout behaviour of Weddell seals: consequences for satellite telemetry. Endangered Species Research 10: 83-92

ABSTRACT

An understanding of pinniped haulout behaviour can provide information on how animals interact with their environment, their foraging strategies and the behaviour of their prey. For Weddell seals, knowledge of haulout patterns and the environmental drivers of haulout is comprehensive for the austral spring and summer, but is poorly described outside this period. Pinniped behaviour is commonly examined using satellite telemetry, however it is unclear if the behavioural state of the seal can itself influence data acquisition. We examined haulout behaviour of female Weddell seals *Leptonychotes weddelli* in eastern Antarctica over 3 winters (March - August) using satellite linked data loggers. Haulout behaviour followed a diel cycle with predominantly nocturnal haulouts. The environmental variables wind speed and temperature were influential on haulout, with seals tending to haulout more in lower winds and higher temperatures. Haulout duration decreased across the winter, as did the number of satellite uplinks suggesting that haulout duration played a role in data acquisition. There was no evidence of a decline in tag condition over this period indicating that the decrease in uplinks was primarily the result of the winter behaviour of the seal. Overall, the number of haulout locations in the data set was over represented with more uplinks per hour occurring when hauled out than when at sea. For Weddell seals and other ice seals, tracking data that includes haulout locations can bias spatial representations of foraging behaviour (e.g. haul out sites may be mistaken as regions of area restricted search).

INTRODUCTION

In pinnipeds, "haulout" describes the activity of leaving the water to rest, moult, mate, pup or to escape predators (Thomas and DeMaster 1982; Sato *et al.* 2003b; Bengtson

and Cameron 2004; Mulaudzi *et al.* 2008). Biologists study haulout patterns for both ecological and applied reasons. From an ecological perspective, the duration and timing of haulouts enable inferences on aspects of the seal's environment, such as prey abundance and movement. For example, krill concentrate at the bottom of the water column during the day becoming more dispersed at night, therefore crabeater seals *Lobodon carcinophagus* forage more intensively during the day and haulout at night (Burns *et al.* 2008). If a seal does not haul out for an extended period of time, it may be indicative of an extensive search and therefore infers limited prey availability (*e.g.*, at times of low prey abundance, female fur seals *Arctocephalus gazella* increase foraging trip duration and activity (Boyd *et al.* 1994)). From an applied perspective, haulout patterns have been studied intensively to gain an understanding of the best time of year to undertake population surveys (Carlini *et al.* 2006), and how to best implement monitoring and management plans (Cunningham *et al.* 2009)

In both instances it is also important to know how physical aspects of the environment may influence haulout behaviour, consequently, this is well studied for many species especially throughout the pupping and moulting seasons (Carlens *et al.* 2006). Important factors include temperature, wind speed, solar radiation, lunar cycle, cloud cover, tidal state, substrate and ice cover (Trillmich and Mohren 1981; Schneider and Payne 1983; Reder *et al.* 2003; Sato *et al.* 2003b). Further complicating the influence of environmental factors on haulout behaviour are the underlying diel patterns that have been noted in most seal species (Erickson *et al.* 1989).

Pinniped behaviour, both at sea and hauled out is increasingly examined via satellite telemetry (*e.g.*, crabeater seal *Lobodon carcinophagus* (Burns *et al.* 2004); Baltic ringed seal *Phoca hispida botnica* (Harkonen *et al.* 2008); leopard seal *Hydrurga leptonyx* (Nordøy and Blix 2009)). However, behavioural state may influence the

acquisition of data as transmission conditions are more favourable when the animals are hauled out or in shallow water (Tougaard *et al.* 2008). This leads to the potential of more uplinks or uplinks of a higher quality during haulout. Lake *et al.* (2006) in their study of the winter movements of Weddell seals did not receive locations away from haulout sites. This potential bias may lead to inaccurate biological interpretation of the data received via satellite telemetry such as through the application of movement models (Patterson *et al.* 2008). The potential for haulout behaviour to affect uplinks in this way is complicated by factors such as battery exhaustion, antenna damage and salt-water switch failure which can result in decreases in the number and quality of uplinks and ultimately tag failure (Hays *et al.* 2007).

Here we use satellite telemetry from a study of the winter foraging ecology of Weddell seals to describe the haulout patterns of Weddell seals *Leptonychotes weddelli* outside the pupping, breeding and moulting period (March – August) at two locations in eastern Antarctica over 3 years. In particular, we examine the diel nature of haulout behaviour and the influence of the physical environment for this particularly harsh period. We then determine how haulout behaviour influences the uplink performance of satellite-linked data loggers.

METHODS

Capture, handling and tag deployment

A total of 20 adult, post-moult, female Weddell seals were captured at two locations: Dumont d'Urville (DDU) – 66°40' S, 140°00 E, and the Vestfold Hills - 68°33' S, 78°15' E, over three successive summers: 2006 (n= 9), 2007 (n=6), 2008 (n=5; DDU only) and equipped with satellite relay data loggers (SRDLs) with conductivity,

temperature and depth function (Sea Mammal Research Unit, University of St. Andrews, Scotland). The seals were approached on the ice by foot and temporarily restrained with a head bag or pole net whilst an intravenous injection of zoletil (1:1 mixture of tiletamine and zolazepam) at a dosage of 0.5mg/kg (Wheatley *et al.* 2006a) was administered and the SRDL attached to the head with antenna facing foreward using a two component industrial epoxy. The seal was then observed during recovery from anaesthesia and allowed to enter the water when no longer sedated. The 'winter' period for the purposes of this study are the months March through to August. Haulout behaviour during this time period is not influenced by pupping or moulting. Pupping begins in the last week of September (unpublished data) for DDU and the first week of October for Davis (Lake et al. 1997). Moult has finished by late February in both locations (unpublished data) enabling tags to be deployed from March onwards.

The SRDLs were programmed to record dive depth, dive start time, dive duration and post-dive surface interval every 4s. The tags also recorded the start and end time of each haulout. For each 6h period, the tags recorded the percent time that the animal spent hauled out, diving and cruising. The tag recognised a haulout when it had been dry for 10 min and the haulout ended when the tag was wet for 40s. During haulout, the tag attempted to uplink to overhead satellites every 1min 20s for the first 5h and then cycled off for 6h and on for 1h. At all other times, the tag attempted to uplink every 40s.

General haulout behaviour

The trend in average haulout duration, maximum haulout duration and total haulout duration per seal per month over the winter was examined using a series of linear mixed-effects model in the R package (library *nlme*, function *lme*) distributed under the

GNU general license (http://www.r-project.org). Each of these three response variables were examined in separate models with the fixed variable *month* and *seal* included as a random variable.

To estimate the likelihood of a seal being hauled out at any point in time throughout each month, we calculated the average frequency of haulouts occurring within each hour (*ie.* the local hour at which the haulout started and the subsequent hours spanned across its duration). We then expressed this as a percentage of the total number of haulout events occurring within each hour per seal. The mean, and 95% confidence intervals of these averages were then compared on a monthly basis to detect any changes in the patterns of haulout timing throughout the winter. Average sunrise and sunset for each month at each location was calculated using the R package (library *maptools,* function *crepuscle*) so that haulout behaviour could be interpreted in regard to light conditions.

Detection of diel pattern in haulout

We calculated the number of minutes hauled out for each local hour (0-23) per seal. To determine if there was a cyclic pattern in the time spent hauled out, we then used these data (number of minutes hauled out in each hour) to calculate the autocorrelation estimate between lag 0 and each lag thereafter (i.e. the autocorrelation between hour x and hour $x + 1$, hour x and hour $x + 2$ and so on) for each seal separately using the *acf* function (*stats* package; type = correlation) in the R Package. The *acf* data for all seals was then combined so that the mean autocorrelation and 95% confidence interval at each lag could be calculated.

Environmental influences on haulout behaviour

To examine the influence of weather on haulout, we fitted a series of generalized linear mixed-effect models (GLMMs) to the data using the *lmer* function in the R Package (R Development and Core Team, 2006). GLMMs are linear models that include fixed and random effects. The fixed effects considered for the models were: *wind speed, air temperature, wind chill* (Edholm and Lewis 1964) and *ice concentration. Individual* was included as a random effect. Weather data were sourced from the Australian Government Bureau of Meteorology and were collected for Davis (Vestfold Hills) and DDU station. For all seals and years, the average maximum distance travelled from the base was 68km at Davis and 50km at DDU, so we assumed that the weather at the stations will have been similar to that experienced by the seals. Ice concentration was extracted at all locations provided by Argos (including haulout and at-sea locations) from the daily remote sensing sea ice concentration maps (6.25km grid resolution) retrieved from the Advanced Microwave Scanning Radiometer-Earth Observing System (AMSR-E; Institut fur Umweltphysik Universitat Bremen, http://iup.physik.unibremen.de:8084/amsr/amsre.html).

The model's response variable, *haulout*, was adjusted to be a binary response (*ie.* hauled out or not hauled out) per local hour (DDU = UTC + 10, Vestfold Hills = UTC + 7) to help normalise the data. Wind speed was log transformed to correct for non- Gaussian distribution. Each model contained a binomial error distribution with a logit link. The models were run 100 times on a 10% sub-sample of the data to minimise the temporal auto-correlation within the data.

The model set comprised all of the variables in logical combinations including additive and interaction terms. The best of these models were chosen using information-theoretic model selection procedures, which uses deviance as a measure of fit and

includes a term to penalise more complex models which often fit the data better, but increase the uncertainty in each variable as well as the variance in predictions. We chose to use the change in Bayesian Information Criterion (δBIC) to determine the magnitude of difference between models as opposed to Akaike's Information Criterion (AIC), which is known to have a bias in large sample sizes. The top-ranking model was chosen as the best fit model of the models available if δBIC was greater than two.

Effect of haulout behaviour on satellite uplinks

We examined diagnostic data supplied by Argos to determine antenna, battery and salt water switch damage to assess how tag condition may influence the number of uplinks received and therefore differentiate between the influence of haulout on uplinks versus the influence of tag condition on uplinks. Following the methods of Hays et al. (2007) and Lea et al. (2009) we compared the actual number of uplinks achieved for each tag to the expected number of uplinks (80,000) to ascertain if the relayed number of uplinks was within 90% of the expected number of uplinks. If so, the battery was assumed to have drained. The running averages describing the driest condition of the salt water switch were examined to detect a progressive reduction towards 50 indicating the build up of bio-fouling and the number of times the wet-dry sensor failed was examined to determine salt water switch failure. Finally, the best level reading was examined to detect any erratic or steep decline towards the end of the tags life indicating antenna failure.

To determine if haulout behaviour influenced the number of uplinks, we quantified the time spent hauled out per seal per month and the total uplinks per seal per month with a linear mixed model (*nlme* package) in the R package. *Number of uplinks*

was the response variable modelled against the fixed variable, *total haulout duration*, with *seal* as the random variable.

To determine the conditions under which an uplink was unlikely, we used the 6h behaviour summaries, retaining only days in which all 4 summaries were complete so that each seals daily activities could be represented as proportion of time spent hauled out and proportion of time at sea (time spent diving + time spent cruising). We then determined if an uplink did or did not occur in this daily period and applied a GLMM to the data in the R package (*lmer* function, binomial error distribution and logit link). The binomial response variable, *uplink*, was modelled against the fixed variable *time spent at sea* with *seal* as a random variable.

To examine if haulout behaviour has the potential to lead to spatial misinterpretation of the data (*i.e.* whether haulout locations are over or under represented in the data), we determined how many uplinks overall corresponded to times at which the seal was hauled out and times at which the seal was at sea. We then determined the time spent at sea and hauled out per seal per month which enabled the calculation of number of uplinks per hour when at sea and number of uplinks per hour when hauled out on a monthly basis per seal. These monthly values were averaged for each seal resulting in a value of uplinks per hour hauled out and uplinks per hour at sea for the entire winter period per seal. These values were then compared using a paired t-test in the R package to determine if number of uplinks occurring when hauled out differed significantly to number of uplinks occurring when at sea.

RESULTS

Of the 20 tags deployed, data from 5 tags were excluded from this study as they did not provide an adequate representation of the 'winter' period (deployment details for the 15 tags included in this study can be found in Table 2.1).

Table 2.1 Summary of deployment for the 15 seals included in this study detailing location of deployment (DDU = Dumont d'Urville; VH = Vestfold Hills), date of deployment, date of last uplink and deployment duration.

Seal ID	Location	Date of deployment	Last uplink	Duration of deployment (days)
ct38w-Denise-08	DDU	22/2/2008	2/11/2008	254
ct38w-Elodie-08	DDU	21/2/2008	29/4/2008	68
ct38w-Mathilde-08	DDU	21/2/2008	18/10/2008	240
ct38w-QueenEliz-08	DDU	21/02/2008	22/8/2008	183
wd3-CTD1-07	DDU	20/2/2007	7/11/2007	260
wd3-CTD2-07	DDU	20/2/2007	21/8/2007	182
wd3-CTD3-07	DDU	21/2/2007	20/9/2007	211
awru1-A-06	VH	1/3/2007	29/7/2007	150
awru1-B-06	VH	1/3/2007	2/10/2007	215
awru1-C-06	VH	1/3/2007	11/8/2007	163
wd1-10165-06	VH	15/2/2006	5/6/2006	110
wd1-10183-06	VH	17/2/2006	9/7/2006	142
wd1-10213-06	VH	16/2/2006	8/10/2006	234
wd1-10216-06	VH	19/2/2006	27/4/2006	67
wd1-10217-06	VH	17/2/2006	13/6/2006	116

General haulout behaviour

Over the 3 years of this study, we recorded 2074 haulout events from 15 seals averaging 3.9 ± 0.1h (mean ± se) in duration and ranging from 0.15 to 23h. The average interval between haulouts was 24.44 ± 0.59h. Sixty two percent of intervals were less than 24h, however intervals were as long as 8 days. Seals spent on average 20 ± 0.5% of their time hauled out.

Total time hauled out each month for each seal decreased from March (150 ± 15.7h) through to September (86 ± 11h; ANOVA $F_{1,57} = 37.42$, $P < 0.0001$; Table 2.2).

However, the average and maximum haulout duration did not differ significantly with month (average haulout duration ANOVA $F_{1, 57} = 0.33$, $P = 0.57$; maximum haulout duration ANOVA $F_{1, 57} = 3.06$, $P = 0.085$), indicating a decline in number of haulouts per seal per month (Table 2.2).

Table 2.2 Winter haulout summary (mean ± se): total haulout duration, average haulout duration, maximum haulout duration and average number of haulouts per seal per month with sample sizes for each month (n).

Month	Total haulout duration (h)	Average haulout duration (h)	Maximum haulout duration (h)	Average number of haulouts	n
March	150 ± 15.7	4.75 ± 0.50	14.1 ± 0.63	30.5 ± 2.95	15
April	112 ± 9.6	3.98 ± 0.44	14.2 ± 0.72	33.0 ± 3.31	15
May	116 ± 8.68	4.31 ± 0.52	13.7 ± 0.67	23.1 ± 2.21	13
June	92 ± 8.79	4.57 ± 0.70	13.1 ± 1.17	25.6 ± 3.69	12
July	81 ± 10.7	5.07 ± 1.31	12.4 ± 1.35	24.8 ± 2.93	10
August	86 ± 11	3.96 ± 0.79	13.2 ± 0.97	19.8 ± 2.75	9

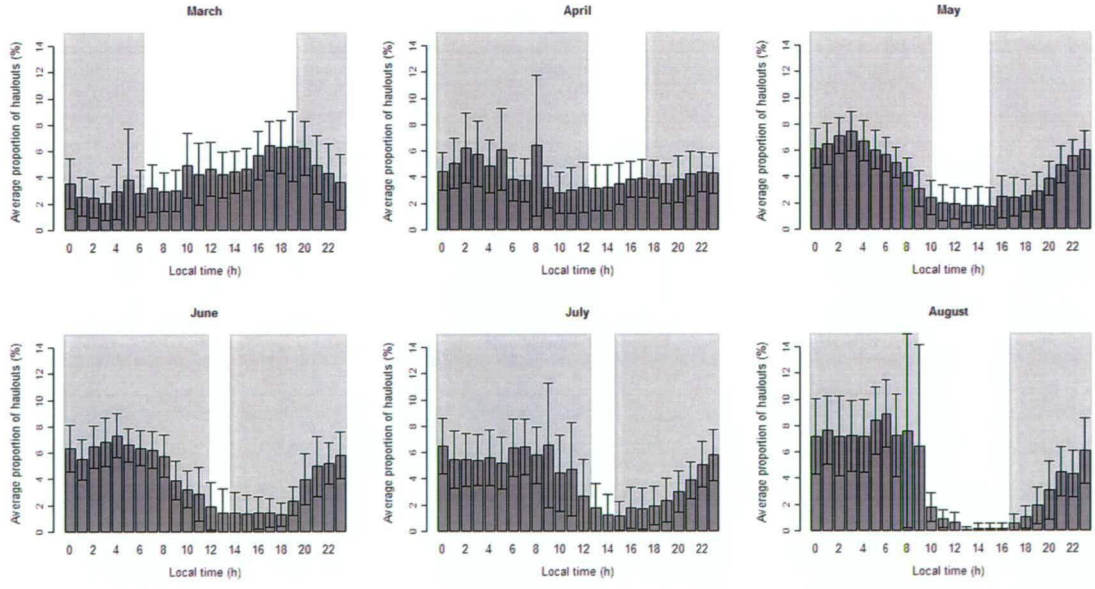


Figure 2.1. The likelihood of a seal being hauled out at each local hour per month expressed as a percentage of the total number of haulout events occurring within each hour per seal with 95% confidence intervals for the months March through to August. The shaded areas indicate nocturnal periods and the unshaded areas indicate diurnal periods.

In March, there was a peak in haulout frequency at approximately 18:00 however from April to August, this pattern shifted to a peak in haulout frequency in the early morning

hours (approximately 02:00 to 04:00) and a minimum at approximately 12:00 to 18:00 (Fig. 2.1). Examination of average time of sunrise and sunset showed that for March, the peak haulout period occurred during the day whilst from April to August, the peak haulout period corresponded to night (Fig. 2.1).

Diel patterns in haulout behaviour

The mean autocorrelation for all seals (Fig. 2.2) indicated decreasing significance of autocorrelation between lag 0 and each lag thereafter (with significant autocorrelation being indicated by any bar above or below the dotted line). Mean autocorrelation peaks again at lag 24. On an individual basis, 11 of the 15 seals demonstrated a significant autocorrelation at lag 24. The 4 other seals demonstrated a peak in autocorrelation at lags 25, 25, 26 and 27 respectively. Overall, the mean autocorrelation plot (Fig. 2.2) indicates that it is highly likely that the behaviour exhibited at lag 0 will be exhibited again 24 hours later.

Influence of physical variables on haulout

The top model used wind speed and temperature (Table 2.3) to explain whether a seal was or was not hauled out. In 70 of 100 iterations log wind speed and temperature were the top model, 73% of the time the δBIC was >= 2, with a mean value of 3.20 ± 0.41 (mean ± se). Average wind speed when hauled out (14.4 ±9.91ms^{-1}) was 3ms^{-1} lower than wind speeds when not hauled out (17.4 ± 12.4 ms^{-1}). Temperatures at haulout (-12.8 ± 6.20 °C) were around 0.33°C higher than temperatures when not hauled out (-13.1 ± 6.37°C). The warmest temperatures occurred in March (-8.01 ± 0.14°C; monthly average of temperature across sites) followed by a steep decline in temperature through

to July (-16.4 ± 0.21°C) after which there was an increase in temperature in August (-15.1 ± 0.2°C; Fig. 2.3a). Wind speed was variable across months with May experiencing the strongest winds (18 ± 0.43 ms^{-1}; monthly average of wind speed across sites) and July experiencing the lightest winds (15.2 ± 0.4 ms^{-1}; Fig. 2.3b).

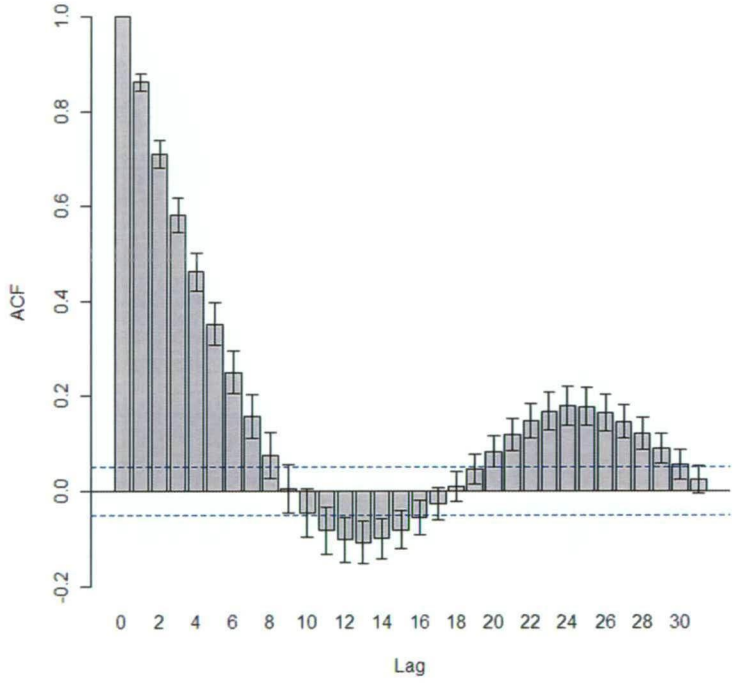


Figure 2.2. Mean autocorrelation plot of haulout behaviour for all seals with 95% confidence intervals. Any bar reaching above the dotted line is correlated with lag 0. Correlation declines towards lag 12 and peaks again at around lag 24 indicating a diel cycle in haulout behaviour.

Table 2.3 Results from 100 iterations of the GLMM: the number of times the model was top model (Frequency) and variables comprising that model

Frequency	Variables
70	log wind speed + temperature
14	log wind speed + temperature + log wind speed * temperature
13	log wind speed
1	ice concentration + log wind speed + temperature
1	ice concentration + log wind speed + temperature + log wind speed * temperature

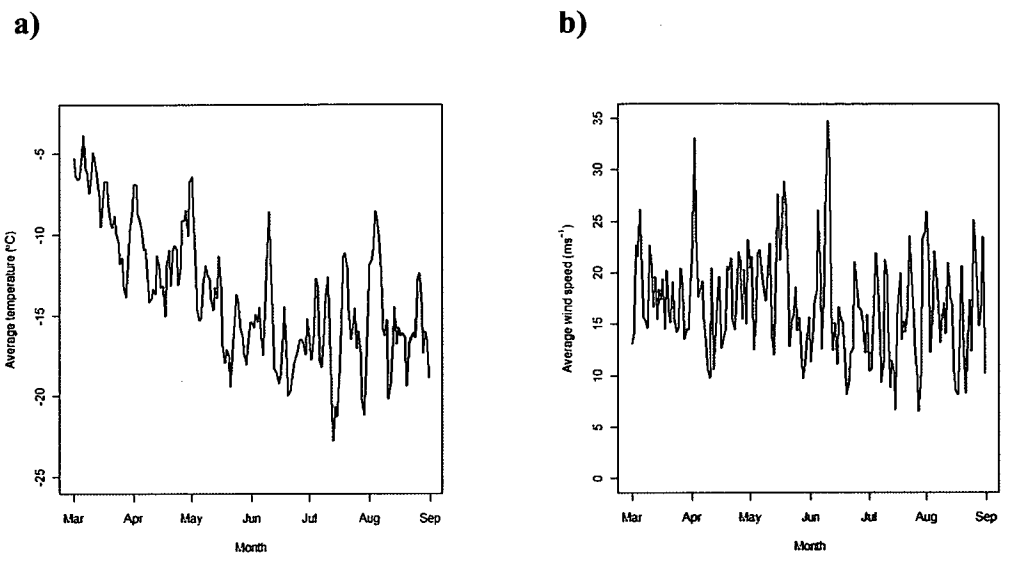


Figure 2.3. (a) Average daily temperature for Dumont d'Urville and the Vestfold Hills across the study period and (b) average daily wind speed for Dumont d'Urville and the Vestfold Hills across the study period.

Effect of haulout behaviour on satellite uplinks

Failure due to salt-water switch failure or battery exhaustion was not detected in any of the 15 tags. For 2 tags, failure could be attributed to antenna failure evident within approximately the last 25 days of the tags life. For both tags this corresponded to the month of October, which was not included in analyses as it was outside the March to August period of interest.

There were a total of 21,944 uplinks over the months of March to August for the 15 seals (an average of 1462 ± 311 uplinks per seal). The average number of uplinks per seal per month decreased from March (422 ± 63) to August (260 ± 108) (ANOVA $F_{1,56}$ = 29.65, $P < 0.0001$; Fig. 2.4a).

The longer a seal spent hauled out per month, the greater the number of uplinks (ANOVA $F_{1,56}$ = 59.69, $P < 0.0001$, Fig. 2.4b). Greatest total time spent hauled out occurred in March (150 ± 15.7h), which corresponded to the month of greatest average number of uplinks per seal (422 ± 63) as opposed to the month of July in which total

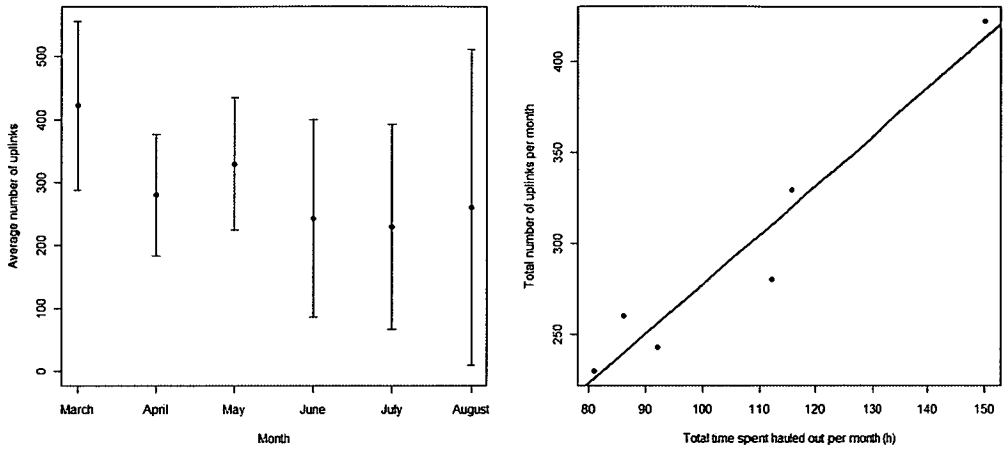


Figure 2.4 (a) Average number of uplinks per seal per month with 95% confidence intervals demonstrating a decline in uplinks as the study period progresses (ANOVA $F_{1,56} = 29.65$, $P < 0.0001$) and (b) Average total haulout duration per seal per month in relation to the average number of uplinks per seal per month (linear regression $F_{1,4} = 57.28$, $P = 0.002$, Adj. $R^2 = 0.92$).

time spent hauled out was lowest (81 ± 10.7h) as were the average number of uplinks per seal (229 ± 71.9) therefore fewer uplinks occurred as total haulout duration decreased. An uplink was most likely on days when the seal spent less than 81 ± 0.44% of the time at sea, and least likely when spending more than 95.8 ± 1.35% of the day at sea (BIC = 417.1, log likelihood = -197.5, deviance = 395, P = 0.0000017). A greater number of uplinks occurred during haulouts (0.67 uplinks per hour) than when at sea (0.35 uplinks per hour; $t = 2.69$, $p = 0.02$ (2-tailed), $df = 10$; Table 2.4).

Table 2.4 Average time spent hauled out as a percentage of total time available per month, average percentage of uplinks occurring at haulout in relation to total number of uplinks, average percentage of uplinks occurring at sea in relation to total number of uplinks, average number of uplinks per hour when hauled out and average number of uplinks per hour when at sea per seal per month (all expressed as mean ± se).

Month	Average time hauled out (%)	Average uplinks at haulout (%)	Average uplinks at sea (%)	Average uplinks/h at haulout	Average uplinks/h at sea
March	20.2 ± 0.02	16.6 ± 2.12	83.4 ± 7.2	0.52 ± 0.08	0.66 ± 0.07
April	15.6 ± 1.33	29.8 ± 6.44	70.2 ± 7.82	0.72 ± 0.14	0.32 ± 0.04
May	15.6 ± 1.17	27.3 ± 5.1	72.7 ± 14.5	0.86 ± 0.22	0.34 ± 0.07
June	12.8 ± 1.22	24.7 ± 7.53	75.3 ± 13.4	0.59 ± 0.11	0.27 ± 0.05
July	10.9 ± 1.45	20.5 ± 7.45	79.5 ± 16.6	0.52 ± 0.18	0.21 ± 0.04
August	11.6 ± 1.48	23.6 ± 9.5	76.4 ± 25.7	0.64 ± 0.25	0.22 ± 0.08

DISCUSSION

Winter haulout behaviour

Few aspects of the winter behaviour of Weddell seals have been described. However, many studies have described haulout throughout the austral spring and summer, reporting haulout as a diurnal event with a peak in mid to late afternoon (Smith 1965; Stirling 1969c; Siniff *et al.* 1971; Thomas and DeMaster 1983; Lake *et al.* 1997; Sato *et al.* 2003b). Only Kooyman (1975) has noted haulout patterns outside of this period which he found to be nocturnal. With the exception of the month of March, we also detected a tendency to haulout nocturnally throughout the 'winter' period. For the Weddell seal, it seems there is a switch in haulout behaviour between the austral spring and summer period to the autumn and winter period. We also detected a diel pattern of haulout, indicating that each haulout occurs at a similar time among the seals. The timing of haulout - whether it is nocturnal or diurnal, whether it occurs at a regular or irregular time or whether it is protracted or short, has the potential to infer information on the activities of the seal (*i.e.* pupping), the foraging environment (*i.e.* prey availability) and environmental conditions (*i.e.* temperature).

Haulout behaviour was greatly influenced by biological events occurring throughout the austral spring and summer. Haulout behaviour is initially modified as Weddell pups are born and nursed on the ice (Thomas and DeMaster 1983) in late September to early October for DDU (unpublished data) and the Vestfold Hills (Lake *et al.* 1997). Then during moult, which may start as early as January, and is usually finished by March (unpublished data), the peak in haulout at mid afternoon when solar radiation is at its greatest allows for a more efficient moult as skin temperature is increased (Feltz and Fay 1966; Schneider and Payne 1983; Boily 1995). Nocturnal

haulout as a general behaviour has been described for a number of Northern hemisphere seals including the Saimaa seal *Phoca hispida saimensis* (Kunnasranta *et al.* 2002), the Baltic grey seal *Halichoerus grypus* , captive Harp seals *Pagophilus groenlandicus* (Moulton *et al.* 2000) and Baltic ringed seals *Phoca hispida botnica* (Harkonen *et al.* 2008) and in these cases, was attributed as a response to prey behaviour, disturbance and weather.

A switch from diurnal (summer) to nocturnal haulout behaviour (winter) has also been described for crabeater seals *Lobodon carcinophagus* (Burns *et al.* 2004) along the western Antarctic Peninsula. This switch reflects prey behaviour throughout the winter period, as the seals concentrate foraging effort during the day and at depths close to the bottom to access prey (zooplankton) and haul out during the night when foraging opportunities are more limited due to a more dispersed distribution of their prey. The winter prey of Weddell seals, which includes *Pleuragramma antarcticum*, benthic fish and prawns (Lake *et al.* 2003), may feed on zooplankton, and therefore be aggregated during the day. If this were the case, it would be more profitable for Weddell seals to concentrate foraging effort during the day.

Whilst the timing of haulout may be determined by prey behaviour, it can also be due to the foraging strategies of the predator. Weddell seal's eyes are modified to function in low light conditions with a high degree of summation (Pütter 1903) and only rod shaped receptors (Landau and Dawson 1970). Weddell seals use the under-ice surface for backlighting when foraging (Davis *et al.* 1999) indicating that vision is important to this predator. Assuming vision is vital to the successful foraging of the Weddell seal, periods of low light availability would adversely impact on foraging and therefore the seal would be more likely to spend these periods doing other activities such as haul out. We hypothesise that for this visual predator, there is a distinct

advantage to hunting during the time periods of highest light throughout the light-limited winter months. Concurrently, these periods of highest light in the winter may be associated with certain prey behaviour (as discussed for zooplankton by Burns *et al.* 2004) that increases the potential for foraging success.

Physical factors related to thermoregulation also influence the winter haulout behaviour of Weddell seals, which are more likely to haulout under conditions of low wind speed and relatively higher temperature. This suggests that the "wind chill" effect (the combination of wind speed and temperature) influences haulout. However, the wind chill calculation (Edholm and Lewis 1964) we included in the general linear mixed effects model was derived to describe the relationship between wind speed, temperature and heat loss in humans living in polar regions. Consequently wind chill was not correlated with haulout and therefore was not an appropriate index to describe the combined effect of wind speed and temperature on Weddell seals. Haulout under conditions of higher temperature and lower wind speed has been noted previously for the austral spring and summer (Cornet and Jouventin 1980; Lake *et al.* 1997; Sato *et al.* 2003b) however, in winter, the warmest temperatures are far colder than summer temperatures. Weddell seals have a thick subcutaneous blubber layer that together with peripheral vasoconstriction, allows them to remain homeothermic in cold water (Boily 1995) and thermoneutral to at least -7°C (Noren *et al.* 2008). This results in a lack of nutrients and oxygen reaching the epidermis and epidermal metabolism is slowed or inhibited. Epidermal maintenance most notably occurs during summer (moult) when the thermal requirements of the epidermis can be satisfied on land (in air) where the heat flux is twenty-five times lower than in water of the same temperature (Noren *et al.* 2008). Promoting blood flow to the epidermis may be an advantage of hauling out during winter under conditions of low wind speed and high temperature.

Effect of haulout behaviour on satellite uplinks

Ideal conditions for uplink to overhead satellites are often sustained during haulout as compared to intermittent opportunities when regularly diving at sea. For tagged animals that inhabit fast ice, uplinks may be limited further by the lack of open water through which the tag can be lifted to the surface to uplink to overhead satellites. Therefore, haulout behaviour has the potential to influence how many uplinks occur and how the data collected is interpreted due to the potential for haulout locations to be over represented within the data set (Lake *et al.* 2006).

Total time hauled out each month declined as winter progressed, as did the number of uplinks per month. This may be a direct relationship moderated by physical factors such as wind chill, which increases as winter temperature continues to decline and wind speed increases (and therefore results in fewer or shorter haulouts). In this case, haulout behaviour influences the number of uplinks due to the positive relationship between haulout duration and number of uplinks. However, it is possible that this decline in uplinks may also be influenced by tag condition. Salt water switch failure, which is often due to bio-fouling of the salt-water switch, may account for a reduction in uplinks (Hays *et al.* 2007) but was not detected for the tags deployed in this study. There is considerable potential for antenna damage as the antenna is routinely knocked and forced through ice when Weddell seals maintain, breath and haulout through ice holes or ice cracks in the winter. We detected antenna damage for two tags after 200 days of deployment indicating that the antennas can withstand the rigours of the Antarctic winter and did not influence the occurrence of uplinks. No tag reached a point where it had exhausted its battery as indicated by the number of uplinks obtained per tag. The battery itself can operate throughout a wide range of temperatures (85°C to -60°C - specification sheet can be found at

http://www.saftbatteries.com/Produit_LSH_cell_range_303_8/Language/en-US/Default.aspx#DL2) therefore the cold conditions under which it operates should not influence battery life or function. At low temperatures, voltage can collapse, causing the tag to reset, however, SMRU SRDLs protect themselves by suppressing transmissions below -15°C. This may contribute to the decreased number of uplinks throughout the months of May, June, July and August that routinely experience temperatures lower than -15°C (Fig. 2.3a). Haulout duration decreased across this same period therefore differentiating whether a decrease in uplinks is due to transmission suppression or due to haulout behaviour is virtually impossible. However, our data indicates that Weddell seals tend to haulout in warmer conditions, which makes it likely that uplinks will occur during haulout. When uplinks occur at sea, the tag comes to the surface exiting a water temperature of around -1.8°C. Once again, it is likely that uplinks will occur initially before cooling to the ambient temperature.

Satellite pass schedule may also influence a tag's potential to uplink to overhead satellites. If the majority of satellites pass nocturnally when haulout is more likely then there is greater potential for an uplink. Unfortunately, the historic satellite pass schedule is not available however there are currently 6 satellites that pass approximately 10 times a day (therefore approximately 60 passes a day) and each pass can range from just a few minutes to 15 minutes (CLS Argos).

Lake *et al.* (2006) suggest that even though head attachment of transmitters is the optimal method to ensure locations collected in the water as well as hauled out, this attachment may result in the inability to use small breathing holes, undermine networks of breathing sites and winter foraging behaviour, and ultimately affect survivorship. However, our study demonstrated that head attachments did not affect the ability of seals to access breathing holes throughout the winter months: seals spent 80% of their

time at sea and 77% of all locations received were at sea where the opportunity for uplinks presumably occurred when the seal accessed a hole, crack or open water to breathe. In addition, tag deployment duration (Table 2.1) and the available resight data for DDU indicates this method of attachment does not affect survivorship (Vestfold Hills resight data not available). Of the twelve seals tagged at DDU in 2007 and 2008 (seven of which were included in this study), only two remain unaccounted for. Both of these seals are assumed to have been equipped with faulty tags. One tag operated sub optimally (few uplinks of low quality) for 2 months before failure and the other tag also operated sub optimally and failed within the first week of deployment.

There is potential for location information collected by the tags to be biased to haulout locations, as uplinks are more likely when the seal spends less than 81% of its day in the water. Weddell seals do not necessarily haulout next to their foraging site and attempts to detect foraging areas may be influenced by a predominance of haulout locations (Lake *et al.* 2006). Our analyses confirm that there is a bias in the number of uplinks occurring at haulout (0.67 uplinks per hour as opposed to 0.35 uplinks per hour when not hauled out) and therefore there is over representation of haulout locations within this data set. Tracking data is often used to describe foraging behaviour and identify important foraging locations through techniques that assess the amount of time spent within a certain area (*e.g.* area restricted search). For ice seals such as the Weddell seal that do not return to a central haulout site, tracking data contains locations when hauled out and locations when at sea. This contrasts to the tracks of other seals, generally described as central place foragers that return to a central haulout site. For a central place forager, each time at sea can be regarded as a 'trip' and the track can be broken down into multiple 'trips' comprising of locations at-sea. When a seal is hauled out, it is not foraging yet these over represented haulout locations are often included

when assessing important foraging areas for ice seals. Therefore, if tracking data is used to identify important foraging sites and describe general foraging behaviour of ice seals that frequently haul out, there is the potential for the results to be misleading. We can go some way to addressing this over representation of haulout locations in the data set quite easily by simply differentiating between haulout locations and at sea locations and then modifying analyses accordingly. For example, haulout locations may be removed completely when constructing the track to identify foraging behaviour. When identifying area restricted search through any of the multitude of methods available, haulout locations can be initially assigned to a behaviour class such as 'rest' or 'haulout' and therefore excluded from being classed as a 'search' behaviour.

Conclusions

For the months April through to August, Weddell seal haulout is predominantly nocturnal and each haulout occurs at a similar time. Total monthly haulout duration declined across the same period. Both temperature and wind speed influenced the timing of haulout with seals more likely to haul out under conditions of low wind and high temperature. Therefore it is likely that the timing of haulout is partly governed by thermoregulatory requirements. Other potential hypotheses to explain timing of haulout from March to August involve behaviour of both predator and prey.

The number of uplinks per month declined across the March to August time period relative to the decline in haulout duration per month indicating that haulout duration and the number of haulouts influences number of uplinks. An uplink was more likely when a seal spent less than 81% of its day at sea. The number of uplinks per hour when hauled out was greater than the number of uplinks per hour when at sea leading to an over representation of haulout locations within this Weddell seal tracking data set.

For any ice seal that routinely hauls out, there is the potential for this same bias towards a predominance of haulout locations, which may lead to inaccurate interpretation of the data and analyses need to be modified to address this.

ACKNOWLEDGEMENTS

We thank S. Blanc, A. Jacquet-Chaboisson, E. Antoine and all volunteers from Dumont d'Urville who assisted in the field. We also thank J. Horsburgh, P. Tucak, L. Clark, J. Kingston and all volunteers who assisted in the field at the Vestfold Hills. We thank all reviewers for providing invaluable comments and suggestions to improve this manuscript. This study was supported by an Australian Antarctic Science grant (AAS project 2794), and program Terre-Océan-Surface Continentale-Atmosphère from Centre National d'Etudes Spatiales (TOSCA-CNES). We thank the Australian Antarctic Division, Institut Polaire Français Paul Emile Victor (IPEV programs 109 and 394) and Terres Australes et Antarctiques Françaises (TAAF) for providing logistical support and clothing. We are grateful to C. -A. Bost and C. Guinet for their support. Fieldwork and data collection was undertaken with approval from the University of Tasmania Animal Ethics Committee (permit A8523), and from IPEV and TAAF Animal Ethics Committee. All animals in this study were cared for according to their guidelines. V. Andrews-Goff was supported by a Tasmanian Graduate Research Scholarship.

3. Weddell seal movements in the winter ice environment: incorporating a state space approach to account for uncertainty when extracting location-specific environmental variables.

To be submitted as: Andrews-Goff V, Hindell MA, Patterson TA, Field IC, Wheatley KE, Charrassin JB. Weddell seal movements in the winter ice environment: incorporating a state space approach to account for uncertainty when extracting location-specific environmental variables.

ABSTRACT

Advances in the field of satellite telemetry and biologging have lead to the ability to use animal locations to gain an understanding of how animals use and interact with their environment. In particular, they have enabled the study of animals that would have otherwise been impossible to observe, such as marine mammals. Argos locations collected from tagged marine mammals may be subject to substantial location errors. Thus utilisation of environmental variables, such as sea ice concentration, extracted from these locations could lead to a distorted picture of the animal's habitat. We applied a hybrid speed filter and state-space approach utilising a Kalman filter/smoother to Weddell seal tracks to correct Argos location error and then compared these tracks to GPS tracks of the same individuals. Low quality Argos locations B, A and 0 comprised 34.66%, 22.56% and 4.13% of the tracking data set after applying the Kalman filter. The Kalman smoothed locations tracked the GPS locations closely and were on average 3.87 ± 0.56km, 0.18 ± 0.23km and 0.89 ± 0.56km closer to the corresponding GPS location than the Argos location for low quality classes B, A and 0 respectively. When extracting environmental information, use of the Kalman smoothed locations resulted in a correct extraction in relation to the GPS locations 76% of the time as opposed to 65% of the time for Argos locations. We were further able to improve the extraction of environmental information by using the estimated error distribution from the Kalman smoother to extract a weighted mean of the environmental variable. The weighted mean yielded a data set similar to the high quality GPS data set with the bonus of classifying fewer locations as "land." Based on our high-quality GPS locations, these results suggest that the use of location estimates from statistical error-correction methods such as state-space models alone may not be sufficient for robust spatial extraction of high-resolution environmental data. Our results indicate that incorporation of location error

into the extraction of environmental data weighted by the uncertainty estimates provides an accurate picture of environmental use, which should improve interpretation of the role of the environment in animal behaviour when high quality animal locations are not available. This is especially true for analysis of historic Argos tracking data sets pre-dating GPS tracking.

INTRODUCTION

Marine birds and mammals present unique challenges to satellite telemetry and biologging due to the inherent uncertainty associated with animal locations. The Argos satellite system is commonly used to track marine mammals and relay other behavioural or environmental information collected by tags (Vincent *et al.* 2002). However, as these animals spend most of their time underwater where communication with an Argos satellite is impossible, the uplink success rate is lower than the success rate in terrestrial applications (Vincent *et al.* 2002).

Knowledge of how an animal exploits and is influenced by its environment is an essential component of foraging ecology (Pinaud and Weimerskirch 2005) and conservation (Villegas-Amtmann *et al.* 2008). For marine animals, this information can be defined using locations derived from the Argos satellite system to extract location-specific information on the environment. This information includes but is not limited to sea surface temperature (Guinet *et al.* 1997; Lea and Dubroca 2003), chlorophyll distribution (Lea & Dubroca 2003), bathymetry (McConnell *et al.* 1992) and sea ice concentration (Bradshaw *et al.* 2004). However, as there is varying spatial error associated with Argos locations, it is likely that environmental information extracted at the Argos location may in fact be different to that being experienced by the animal at its

true location. The consequence is a distorted picture of habitat use and the influence of the environment on animal behaviour.

For each Argos location, an estimated error is calculated when at least four messages are received during a satellite pass (Service Argos 2010). A location class (LC) is assigned to each location based on this estimate of error. LC 3 has an estimated error of < 250m, LC 2 has an estimated error between 250 and 500m, and LC 1 has an estimated error between 500 and 1500m. LC 0 has an open ended error of > 1500m whilst LC A and B have no accuracy estimation and LC Z is an invalid location. Unfortunately, inaccurate positions (LC 0, A, B, Z) constitute the majority of locations in marine mammal tracking datasets (Freitas *et al.* 2008d). For example, the proportion of low quality locations occurring in the tracks of the nine different marine mammal species analysed by Freitas *et al.* (2008d) was at best 69% (belugas and Antarctic fur seals) and at worst, 93% (southern elephant seals).

Environmental data sets typically used in conjunction with animal tracking information are available on various scales including kilometres (AMSR-E sea ice concentration - http://www.iup.uni-bremen.de:8084/amsr/amsre.html), metres (MODIS sea ice images - http://nsidc.org/data/iceshelves_images/), minutes (ETOPO1 - http://www.ngdc.noaa.gov/mgg/global/global.html) and seconds (GEBCO 30s bathymetry - http://www.gebco.net). However, as remote sensing technology improves, the trend is towards higher resolution environmental data sets. Given there is the potential for over 50% of locations to have an error in excess of 1500m within a marine tracking data set, the extraction of associated environmental information such as ice concentration and bathymetry may lead to misleading conclusions. Despite the fact that many studies have investigated animal-environment interactions using this approach, this important problem has not been addressed. This could be a contributing factor to

the generally poor fit of models relating animal movement to environmental features, particularly those attempting to do this at fine scales (Guinet *et al.* 2001; Bradshaw *et al.* 2004).

The Weddell seal is unique amongst the Antarctic ice seals in that it remains close to the Antarctic continent year round (Siniff *et al.* 2008). As the winter ice develops, the Weddell seal becomes constrained to foraging over the Antarctic shelf and must do so under heavy ice concentrations associated with the Antarctic winter. By using Argos locations to extract information on ice concentration, it is possible to investigate how these animals interact with the winter ice environment. In this paper, we account for the spatial error associated with the Argos locations of Weddell seals interacting with the winter ice environment and propose a method to incorporate location error when extracting environmental information such as sea ice concentration. We then use this method to gain an understanding of the winter ice environment that these Weddell seals occupy. Considering the volume of marine tracking data sets generated over the last 30 years, we suggest that these methods will have great utility when analysing historic tracking data sets, pre-dating GPS technology.

METHODS

Capture, handling and tag deployment

Four, post-moult, female Weddell seals were captured at Dumont d'Urville – 66°40' S, 140°00 E over two successive summers: 2006 (n= 2) and 2007 (n=2), and equipped with Mk10 Wildlife Computers Fast GPS tags. The seals were approached on the ice by foot and temporarily restrained with a head bag or pole net whilst an intravenous injection of zoletil (1:1 mixture of tiletamine and zolazepam) at a dosage of 0.5mg/kg (Wheatley *et*

al. 2006a) was administered. Tags were attached to the head with antenna facing forward using a two component industrial epoxy. The seal was then observed during recovery from anaesthesia and allowed to enter the water when no longer sedated.

Each tag was equipped with an Argos transmitter (using Wildlife Computers' Cricket transmitter) and Wildtrack Telemetry System's Fastloc GPS satellite location acquisition, providing both high accuracy GPS locations and standard Argos locations with a corresponding location quality. Wildtrack Telemetry System's Fastloc™ *can* acquire fast GPS constellation signals (< 100 mS) to obtain the relative satellite ranges needed for location calculation to an accuracy of +/- 55m (95%; Wildtrack Telemetry Systems Limited, 2010). Each tag was programmed to obtain a Fast-GPS location every 6h and allowed a maximum of 4 successful Fast-GPS attempts a day. The tag was programmed to suppress Fast-GPS attempts during haulout once a good haulout location had been received.

Argos Kalman filtering

Argos locations were filtered using a combination of heuristic speed filtering and a state-space approach by employing a Kalman filter and smoother (full details of the method are given in Patterson *et al.* (2010)). Briefly, this method applies a speed-filter (McConnell *et al.* 1992) to remove highly aberrant locations from the data set. These are positions that imply implausible speed of travel between locations (in this case $7ms^{-1}$). A random walk model is then fitted to the remaining locations using a Kalman filter to calculate the likelihood of the model. Calibration data collected by Vincent *et al.* (2002) was used to parameterize error distributions for each Argos location class. The Kalman filter relies on Gaussian assumptions and Patterson *et al.* (2010) details a process for truncating the error distributions so that they are

approximately normal. Finally, the Kalman smoother is applied to give interpolated locations at any arbitrary point in time, in this case to coincide with the time of each Argos location. Associated with each predicated Kalman smoothed location is a bivariate Gaussian error ellipse describing the uncertainty surrounding each location.

Due to the sampling program of the Fast-GPS component of the tag, GPS locations could not be matched exactly in time to the Argos/Kalman smoothed location pair. Therefore each Argos/Kalman smoothed pair was matched to its near simultaneous GPS location occurring within the hour of the Argos/Kalman smoothed pair. This assumes that Weddell seal movements over a 1h time scale are small. We propose that this is a safe assumption as swimming speeds derived from the GPS data indicate a maximum swimming speed of $1.2ms^{-1}$ with 95% of the data occurring at or below 0.35 ms^{-1}. Therefore, distance travelled within the hour is 1.26km or less 95% of the time. Each GPS data point was considered as a "true" location and distance to the corresponding Argos/Kalman smoothed pair was calculated.

Andrews-Goff *et al.* (2010) recommended that haulout locations should be accounted for when applying any movement model such as the application of the Kalman filter to raw Argos locations. Whilst Mk10 Wildlife Computers Fast GPS tags have the capacity to assign a GPS location as haulout or not, there was no way of assigning an Argos location as hauled out or not as this information was not provided and Argos locations and Fast-GPS locations did not match in time.

Extraction of environmental information

Sea ice concentration was extracted from AMSR-E sea ice concentration images (http://www.iup.unibremen.de:8084/amsredata/asi_daygrid_swath/l1a/s6250/). Each "pixel" in the image has an allocated ice concentration and is equal to 5.95km X 6.57km. Ice

concentrations were extracted at each Argos, Kalman smoothed and GPS location using the R package (R Development Core Team; library *sp*, function *overlay*).

In addition, at each Kalman smoothed location, a weighted mean of ice concentration [ice] was extracted by weighting each point in the AMSR-E position by the associated error ellipse from the Kalman filter. Therefore, the weighted ice concentration is given by:

$$\overline{[ice]} = \frac{\sum_{i=1}^{n} w_i [ice_i]}{\sum_{i=1}^{n} w_i}$$

where the w_i are weights given by

$$w_i = \frac{1}{(2\pi)|\Sigma_i|^{1/2}} e^{-\frac{1}{2}(\mathbf{x}_j - \mathbf{i}_i)^T \Sigma^{-1} (\mathbf{x}_j - \mathbf{i}_i)}$$

which is the probability density function for a bivariate Gaussian probability density function. Here $\mathbf{x}_j$ is the *j*th grid-coordinate {x-coordinate, y-coordinate} where the ice concentration, $\mathbf{i}_i$ is the point estimate (expected) location from the Kalman filter and $\mathbf{o}_j$ is the estimated variance-covariance matrix from the Kalman filter for the *i*th location.

This process has been graphically represented in Figure 3.1. Figure 3.1a presents a hypothetical environmental surface that is representative of the environmental variable in question, *i.e.* ice concentration, bathymetry or sea surface temperature. In this case note the colour legend that indicates the environmental variable allocated values of between 0 and 100. Figure 3.1b demonstrates the bivariate Gaussian error ellipse describing the uncertainty around a Kalman smoothed location on this environmental surface. The colour legend indicates the probability distribution. Figure 3.1c represents the consequent weighting of the environmental variable according to the error ellipse of

the Kalman smoothed location. The colour legend represents the weighting assigned to each pixel of the environmental surface.

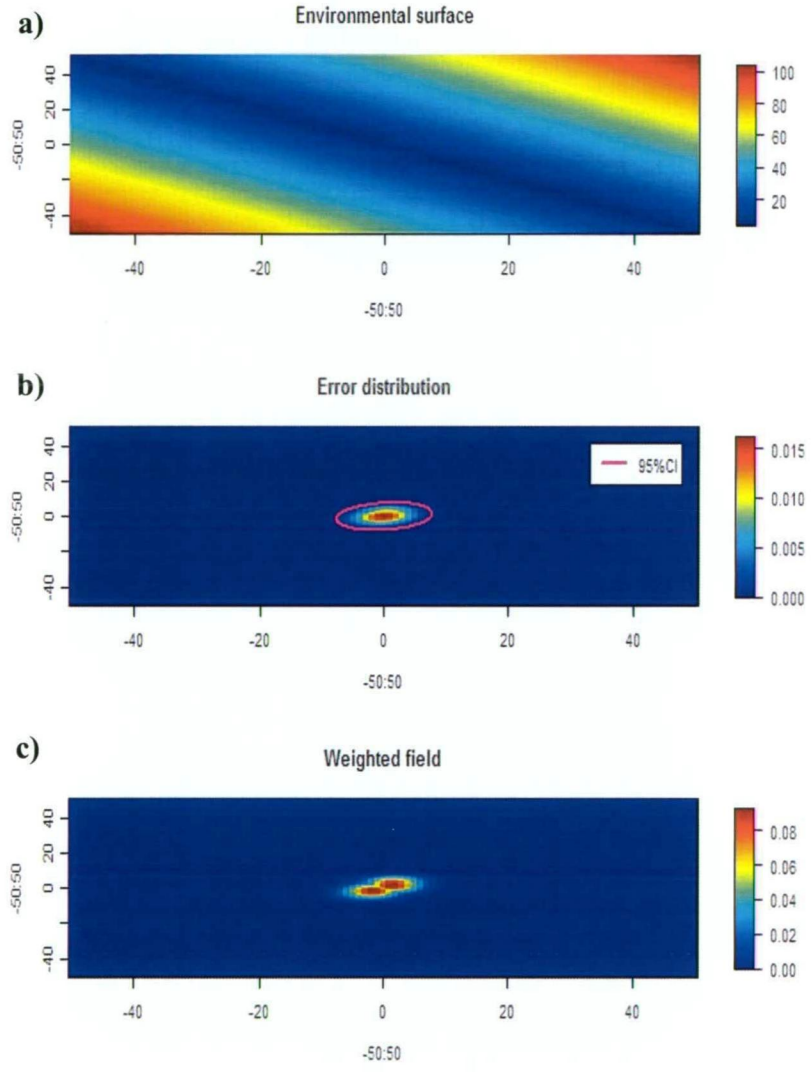


Figure 3.1. The process of applying the Kalman filter and extracting a weighted mean of the environmental variable, **a)** an ambiguous environmental variable spanning a surface from -50:50 (location variable, *i.e.* longitude) and -50:50 (location variable, *i.e.* latitude) on each axis; **b)** the 2D Gaussian error distribution of a Kalman smoothed location occurring on this environmental surface with colour legend representing probability density; **c)** the consequent weighting of the environmental surface using the error distribution of the Kalman smoothed location - the final weighted average value is the sum of the values in panel **c)**, *i.e.* probability animal was at location *x* (derived from panel **b)** * value of pixel at location *x* (panel **a)**).

Weddell seals in the winter sea ice environment

To gain an overall picture of winter ice use by Weddell seals and to assess the ability of the weighted mean to represent the habitat occupied, we examined 20-day composites of MODIS thermal infrared satellite imagery. These thermal images, derived from a compilation of NASA MODIS thermal infrared images have been composited to filter/remove clouds (Fraser *et al.* 2009) and are courtesy of Alex Fraser, Institute of Marine and Antarctic Studies. Each composite represents a 20 day time period and has a resolution of 2km, providing a clear representation of heavy ice (darker areas) and lighter ice (lighter areas) along with ice features such as ice cracks, icebergs, the fast ice edge and so on. For each 20 day period, we provide i) a description of ice habitat use as observed in each high resolution composite according to the corresponding 20 day GPS track with the assumption that both the GPS track and the composite are "true" representations of the ice environment and seal movement, ii) a description of ice habitat use according to AMSR-E ice concentration extraction at each GPS location for the 20 days of the composite and iii) a description of ice habitat use according to a weighted mean extraction of ice concentration over the 20 days of the composite.

RESULTS

Argos location accuracy and the Kalman filter

Weddell seals (n=4) were tracked for a total of 414 days collecting 4217 Argos locations and 1410 GPS locations throughout 2007 and 2008. Of the Argos locations, 64.22% were of low quality having no error estimate (Table 3.1). The highest quality locations, LC 3, account for just over 10% of all locations (11.76%; Table 3.1). After applying the Kalman filter to the Argos locations using a 3h time step, there were 1149 raw Argos locations removed by the speed filter resulting in 9199 Kalman smoothed

locations of which 3000 were time matched exactly to an Argos location. All locations of class Z (n = 68) were removed from the data set as they are regarded as invalid locations (Table 3.1). These 3000 Argos/Kalman smoothed location pairs were then matched to a near simultaneous GPS location resulting in a data set with 723 Argos/Kalman smoothed/GPS locations.

Table 3.1. Percentage of each location class in the raw Argos data set from highest quality location (LC 3) to lowest quality location (LC Z) showing the high percentage of low quality locations in the Weddell seal tracking data set.

Location class	Percentage in raw Argos data set	Percentage after Kalman filtering
3	11.76	11.83
2	13.04	14.45
1	10.98	12.40
0	4.27	4.13
A	22.34	22.56
B	36.0	34.66
Z	1.61	0

The Kalman smoothed locations tracked the GPS locations closely and were a vast improvement on the raw Argos locations (Fig. 3.2). On average each Kalman smoothed location was 1.56 ± 0.09km from its near simultaneous GPS location whilst each Argos location was 3.03 ± 1.56km from its near simultaneous GPS location. Relative to the near simultaneous GPS locations, Kalman smoothed locations derived from low quality Argos locations (LC B, A and 0) were a vast improvement on the raw Argos locations (Fig. 3.3). For LC B, the Kalman smoothed location was on average 3.87 ± 0.56km closer to the near simultaneous GPS location than the matching Argos location, for LC A, the Kalman smoothed location was on average 0.18 ± 0.23km closer to the near simultaneous GPS location than the matching Argos location and for LC 0, the Kalman smoothed location was on average 0.89 ± 0.56km closer to the near

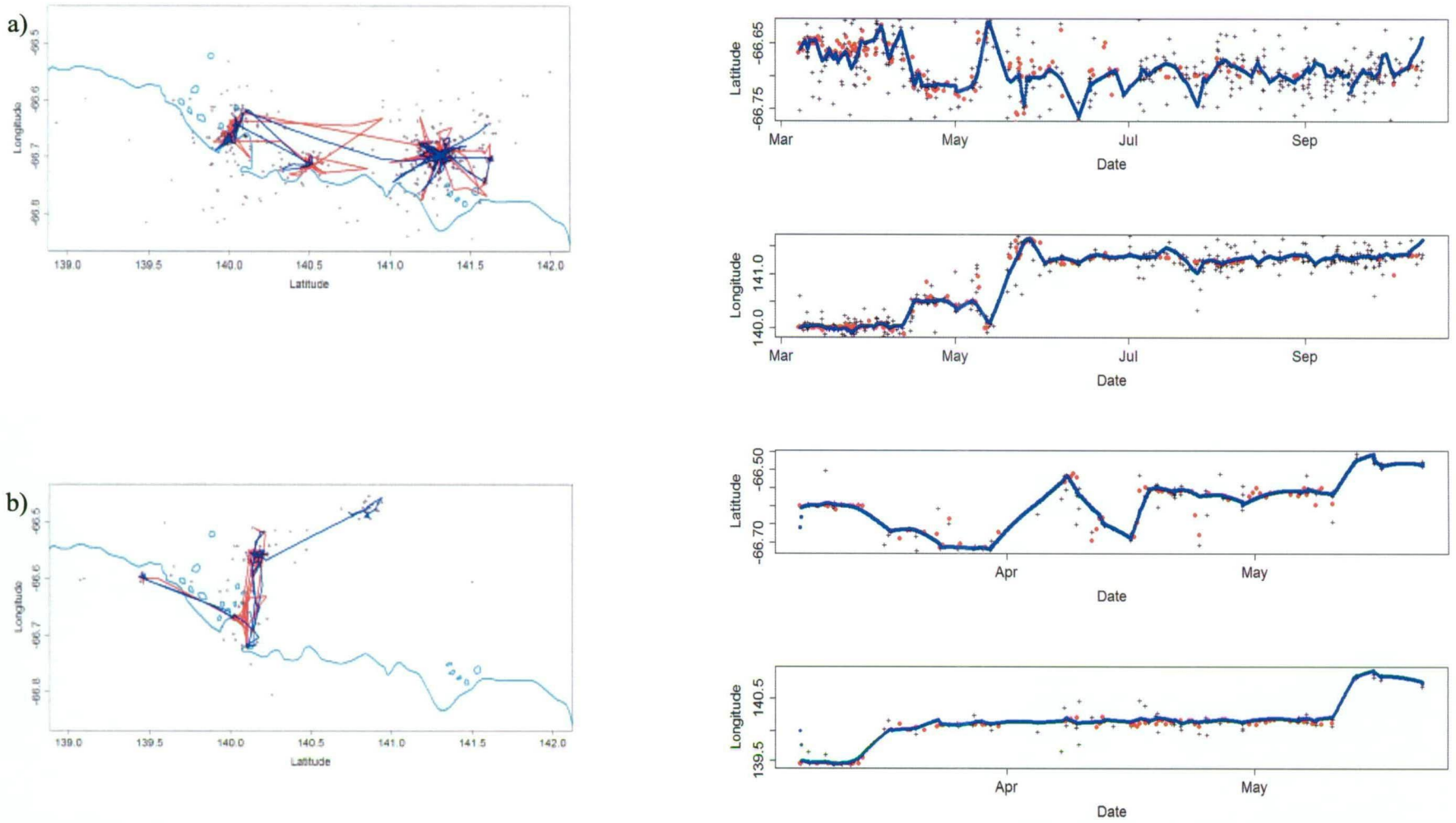


Figure 3.2. Weddell seal tracks for the four Fast GPS tagged seals: a) wd3-W1-07, b) wd3-W2-07, c) ct38w-Aline-Michele-08 and d) ct38w-Delphine-08. Black "+" correspond to Argos locations, blue lines to Kalman smoothed locations and red lines to GPS locations. The scatter of Argos locations across each plot is broad whilst Kalman smoothed locations track GPS locations closely.

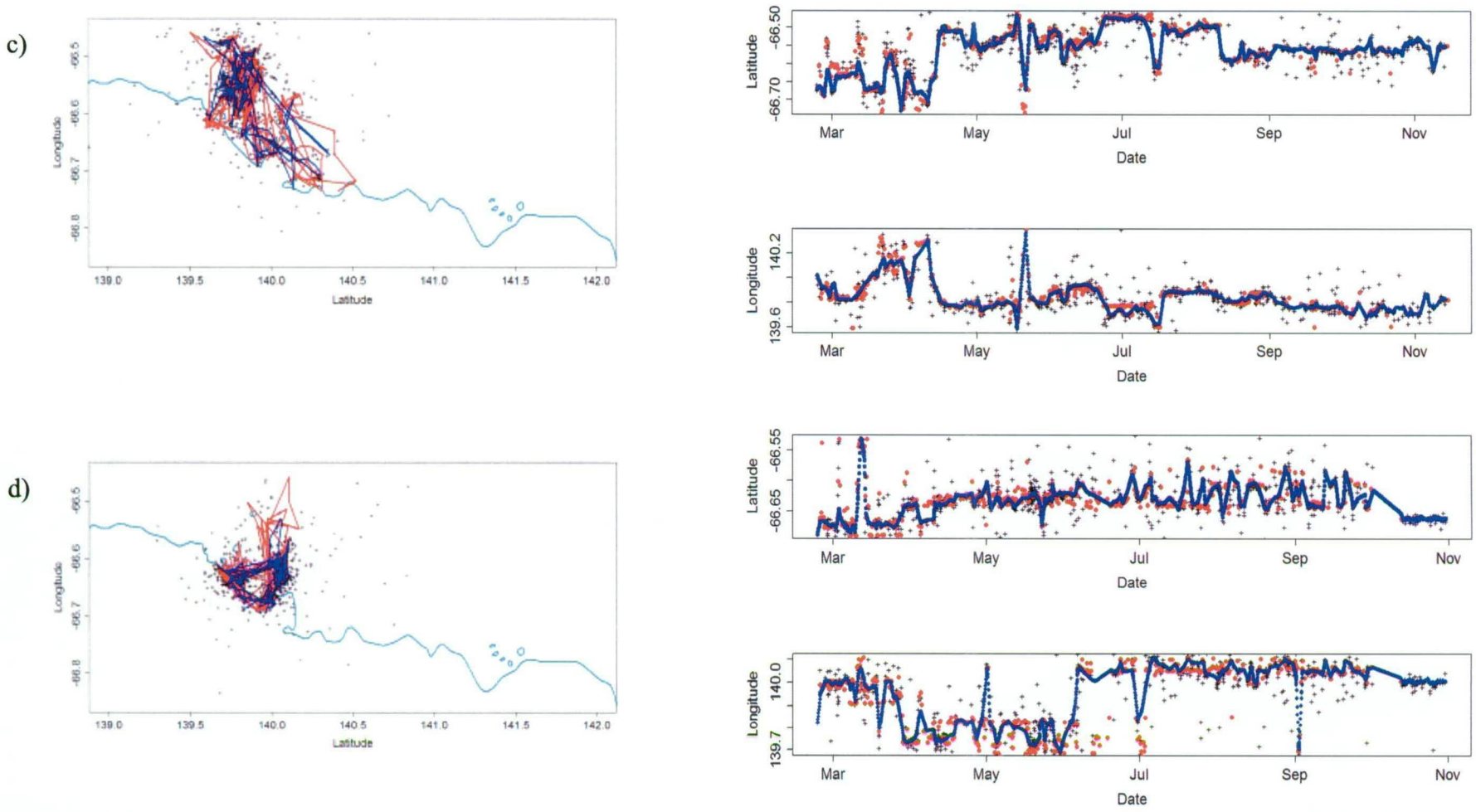


Figure 3.2 continued. Weddell seal tracks for the four Fast GPS tagged seals: a) wd3-W1-07, b) wd3-W2-07, c) ct38w-Aline-Michele-08 and d) ct38w-Delphine-08. Black "+" correspond to Argos locations, blue lines to Kalman smoothed locations and red lines to GPS locations. The scatter of Argos locations across each plot is broad whilst Kalman smoothed locations track GPS locations closely.

simultaneous GPS location than the matching Argos location. For the higher quality locations (LC 3, 2, 1), the improvement of the spatial position of the Kalman smoothed location relative to the matching Argos location was not as marked. For LC 2 and LC 1 respectively, the Kalman smoothed location was on average 0.45 ± 0.10km and 0.13 ± 0.03km closer to the near simultaneous GPS location than the matching Argos location. For LC 3, the highest quality location, the matching Argos location was closer to the near simultaneous GPS location, relative to the Kalman smoothed location by 0.03 ± 0.02km.

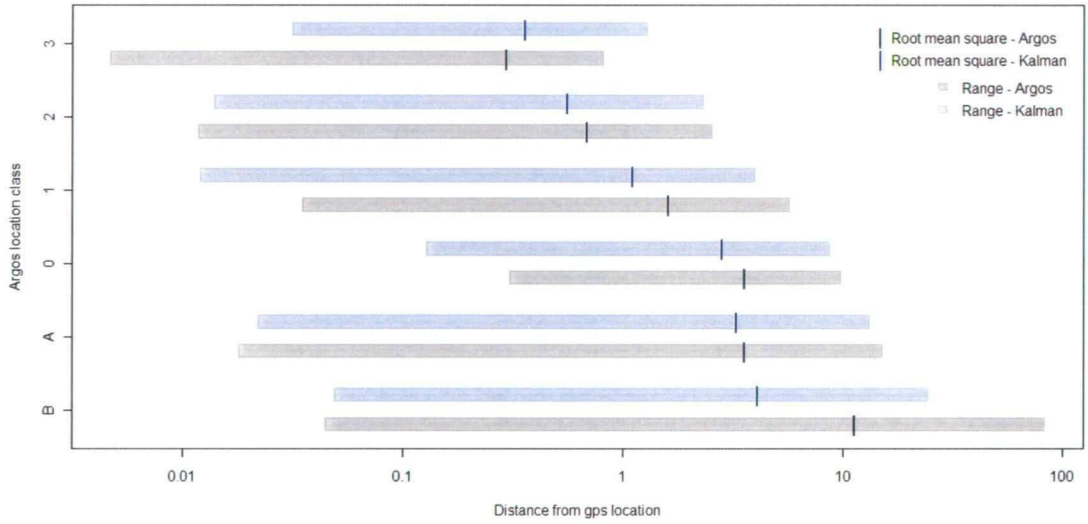


Figure 3.3. Mean root square of the distance between each Kalman smoothed (blue)/ Argos (black) location pair and their near simultaneous GPS location for each location class represented on the y-axis. Note the log scale of the x-axis describing distance from the near simultaneous GPS location. Each vertical solid line represents mean root square, the solid horizontal bar represents the range. The Kalman smoothed location is an improvement on the GPS location for each location class except LC 3.

Spatial error associated with the extraction of an environmental variable

The AMSR-E sea ice images are made up of pixels equivalent to 5949 X 6566m, roughly 6km X 6km (see example image - Fig. 3.5). Ice concentration was extracted for the pixel in which a seal location occurred. For raw Argos locations, 64.73% of all locations occurred within the same pixel as the near simultaneous GPS location. This

improved to 76.21% after they had been Kalman filtered. Therefore, for 27.39% of Kalman smoothed locations and 35.27% of Argos locations, an incorrect extraction of the environmental variable occurred.

If the raw Argos and Kalman smoothed locations were of high quality with low associated error, and given that each AMSR-E pixel is roughly 6km X 6km, we can assume that the high quality raw Argos or Kalman smoothed location would fall within the same pixel or within 36km^2 of the near simultaneous GPS location. If the Argos or Kalman smoothed location were of lower quality and fell in any of the 8 pixels adjacent to the GPS location, they would fall within an area of 9 pixels or approximately 324km^2 of the equivalent GPS location. Following this, if the Argos or Kalman smoothed location were to fall in any of the cells adjacent to these 9 pixels, it would fall within an area of 25 pixels or 900 km^2 and so on. For Kalman smoothed locations, 95% of all locations fell within an area of 9 pixels of the near simultaneous GPS location whilst for the raw Argos locations, 95% of all locations fell within an area of 19 pixels (Fig. 3.4) of the near simultaneous GPS location.

Figure 3.5a is an example of an AMSR-E sea ice concentration image. The inset (Fig. 3.5b) enlarges an area from the AMSR-E image incorporating the edge of the fast ice which graduates into lighter ice and then open water. We have placed an example GPS location on the edge of the open water (Fig. 3.5b) and then examined the 81 pixels (Fig. 3.5c) and 25 pixels (Fig. 3.5d) surrounding this fictional GPS point to demonstrate the representation of ice concentrations within 81 pixels, which is the maximum spatial error associated with the raw Argos locations (at the 99% threshold) in this study, and 25 pixels, which is the maximum spatial error associated with the Kalman smoothed locations (at the 99% threshold). The 99% threshold has been used in this example to demonstrate the potential variability in sea ice concentration possible when considering

99% of all locations. In this example, the fictional GPS location or "true" location is located on a pixel with a 0 – 10% ice concentration.

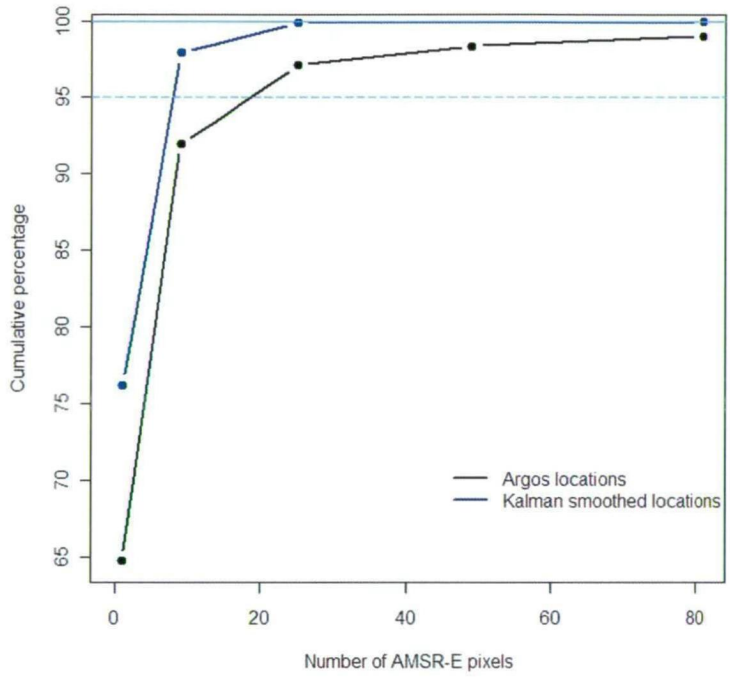


Figure 3.4. Cumulative percentage of the number of AMSR-E pixels in which each Argos (black line) and Kalman smoothed (blue line) location falls in relation to their near simultaneous GPS location with 95% marked with a dashed line and 100% marked with a solid line.

The spatial error associated with the Argos location encompasses ice concentrations ranging from 0 – 50% and 70 – 100% (Table 3.2) therefore the near simultaneous Argos location has the potential to assume an ice concentration anywhere between 0 – 50% and 70 – 100%. Due to its smaller associated error, the Kalman smoothed location has the potential to assume an ice concentration ranging between 0 – 50% which, in this case indicates that the Kalman smoothed location with its lower associated error is a better predictor of the "real" ice concentration than the raw Argos location.

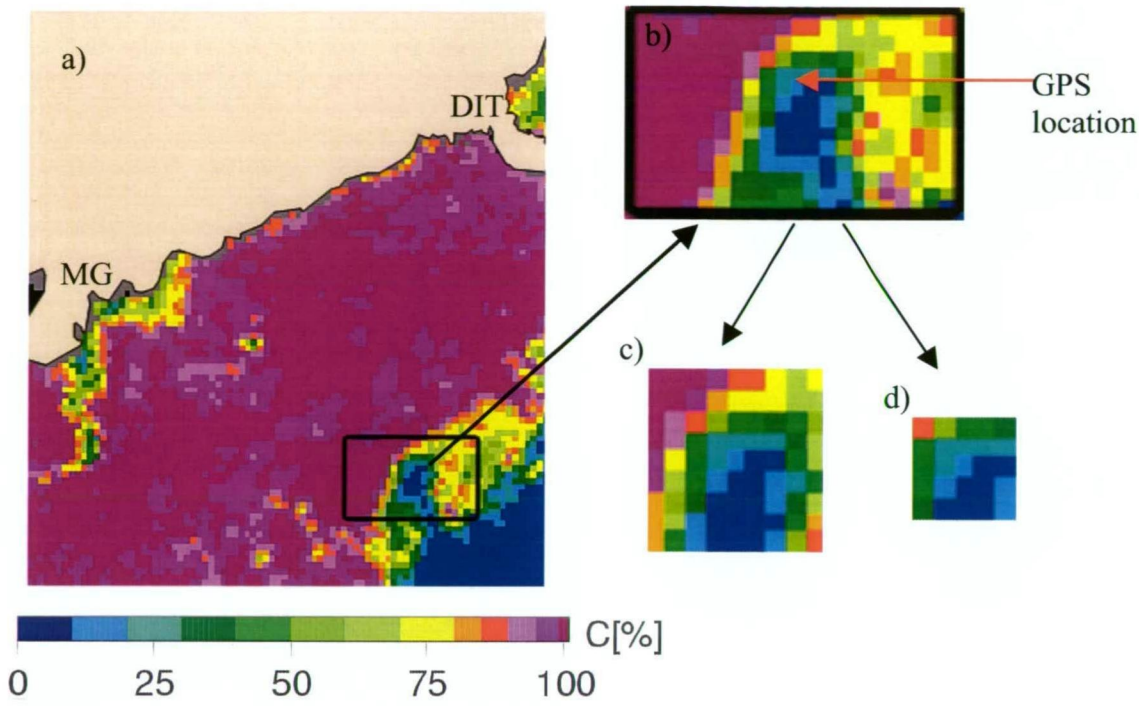


Figure 3.5. Example of an AMSR-E ice concentration image for the 2nd June 2008 illustrating an area spanning from the Mertz Glacier (MG) to the Dibble Ice Tongue (DIT): **a)** large scale image illustrating inset location on the edge of the fast ice; **b)** inset enlargement demonstrating the fast ice edge graduating into open water with red arrow indicating the location of a fictional GPS point; **c)** 81 pixels surrounding fictional GPS point; **d)** 25 pixels surrounding fictional GPS point.

Table 3.2. Ice concentration distribution within the 81 pixel range (Fig. 3.3c) equalling the average spatial error of a raw Argos location and the 25 pixel range (Fig. 3.3d) equalling the average spatial error of the equivalent Kalman smoothed location.

Ice concentration (%)	Distribution within 81 pixels (%)	Distribution within 25 pixels (%)
0 – 10	17.28	28
10 – 20	8.64	16
20 – 30	7.41	20
30 – 40	4.94	8
40 – 50	27.16	24
50 – 60	0	0
60 – 70	0	0
70 – 80	7.41	0
80 – 85	6.17	0
85 – 90	4.94	0
90 – 95	2.47	0
95 – 98	4.94	0
98 – 100	8.64	0

Accounting for spatial error when extracting environmental variables

Ice concentration was extracted directly at each raw Argos location (n = 4217), directly at each GPS location (n = 1410), directly at each Kalman smoothed location (n = 9199) and using the weighted mean method at each Kalman smoothed location. When comparing the results of ice concentration extraction (Fig. 3.6), there are two clear differences between the direct extraction of the Argos, GPS and Kalman smoothed locations in relation to the weighted mean extraction of the Kalman smoothed locations. The first is that the proportion of locations allocated as land in the Argos (Fig. 3.6a), Kalman smoothed (Fig. 3.6b) and GPS data (Fig. 3.6c) set is quite high relative to the weighted mean data set (Fig. 3.6d). This is most likely a reflection of the coastal winter movements of these Weddell seals and the islands present around Dumont d'Urville and Port Martin (66.81°S, 141.38°E; see Fig. 3.2).

For the raw Argos locations, the percentage of locations allocated to land was 20.83% (Fig. 3.6a). For the Kalman smoothed locations, the percentage allocated to land was 14.60% (Fig. 3.6b). Kalman smoothed locations will only be allocated to land if the entire error ellipse associated with the Kalman smoothed location occurs on land. Information on haulout was not provided for raw Argos locations therefore it is not possible to know what proportion of these land locations allocated to the Argos and Kalman smoothed data set were haulouts and likely to be "real" land locations.

For the GPS locations it was possible to determine if locations allocated as land were haulouts. For the GPS data set, 21.78% of all locations were allocated as land however; only 4.20% of all locations were allocated as land and classed as a haulout (Fig. 3.6c). Weddell seals may haulout on land if available making it possible that these land allocations during haulout are 'true' land allocations. Therefore, the percentage of GPS locations potentially incorrectly assigned to land as the animal was in fact at sea

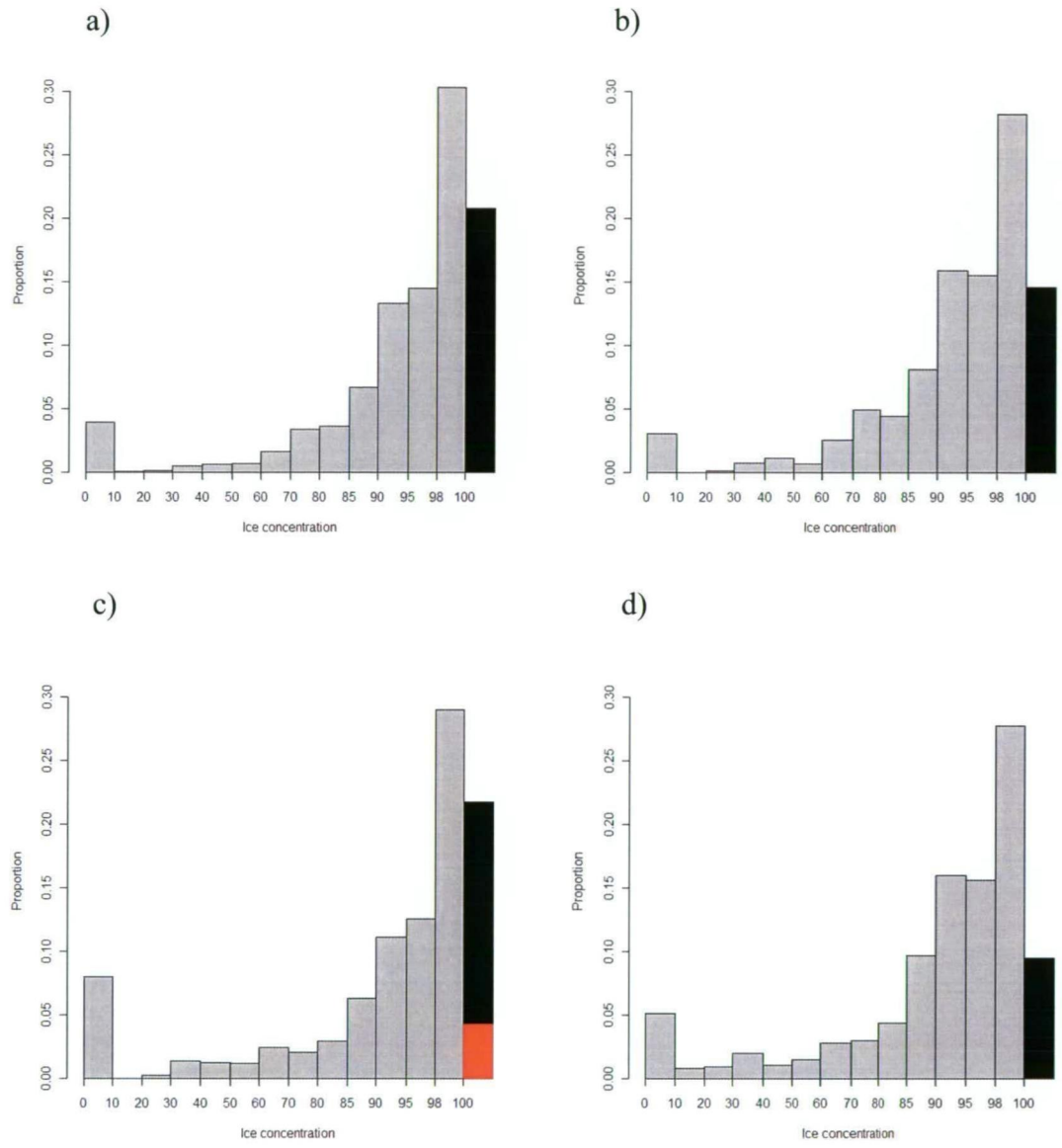


Figure 3.6. Histograms of sea ice concentration extracted at each **a)** raw Argos location (n = 3000), **b)** Kalman smoothed location (n = 9199), **c)** GPS locations (n = 1410) and **d)** Kalman smoothed location using the weighted mean method (n = 9199). The y-axis is proportion of locations and the x-axis is percentage ice concentration. The black bar adjacent to 100% ice concentration represents the proportion of locations that were assigned as land. The red portion of the black bar in the GPS data set **c)** represents land allocations that corresponded to a haulout. The weighted mean data set, **d)**, has a greater proportion of mid range ice concentrations and less locations allocated to land than any of the other data sets.

was 17.58%. Assuming then that 17.58% of GPS locations were incorrectly allocated as land, the mismatch between the spatial resolution of each GPS location (± 55m) and each AMSR-E image (6km X 6km) has to be considered. It is possible that even the fine resolution of a GPS location is not exact enough to allocate correct ice concentrations or land allocations 100% of the time. However, it is also possible that the resolution of the ice image is too coarse and consequently areas at sea were classified as land.

The weighted mean data set that uses the Kalman smoothed locations allocated only 9.47% of locations as land (Fig. 3.6d). Whether these land allocations equate to a haulout cannot be determined. However, this resulted in the weighted mean data set providing an extra 468 locations assigned an ice concentration as opposed to the direct extraction using the Kalman smoothed data set that allocated these locations to land.

These extra 468 locations are the reason for the second prominent difference between direct extraction of ice concentration at each Argos, GPS and Kalman smoothed location as opposed to extracting the weighted mean at each Kalman smoothed location. These extra 468 ice concentrations in the weighted mean data set fall mostly amongst the mid range ice concentrations (Fig. 3.6d). The proportion of high ice concentrations (> 80%) in all data sets is comparable however most similar between the Argos (Fig. 3.6a) and GPS dataset (Fig. 3.6c) and between the Kalman smoothed data set (Fig. 3.6b) and the weighted mean data (Fig. 3.6d). The mid range ice concentrations (10% - 80%) have a stronger representation in the weighted mean data set and are more similar to the GPS data set than either the Argos or Kalman smoothed data sets alone. Assuming the GPS distribution represents the real distribution of ice concentrations accessed, the weighted mean method produces the distribution of mid range ice concentrations most representative of the real ice concentrations. For the very low ice concentrations, 0 – 10%, the weighted mean data set matches the GPS data set most

closely with the Kalman smoothed and Argos data sets underestimating these low concentrations. However, for the high concentrations, > 80%, the weighted mean and Kalman smoothed data sets show less differentiation between the proportion of data assigned to the 90 – 95% and 95 – 98% ice concentrations in relation to the GPS data set. This is probably a reflection of the heavy ice environment that the Weddell seals occupy throughout the winter where ice concentrations classed between 90 – 95% and 95 – 98% would occur in close proximity and extraction at uncertain locations, or using the weighted mean method would "blur" the boundary between these two ice concentration classes.

Overall the weighted mean method provides a comparable data set to the method of direct ice concentration extraction at each GPS location. In the absence of high quality locations, the weighted mean method of environmental extraction will provide a data set representative of the "true" environment but with the tendency to provide more mid-range values. The weighed mean method provides an added bonus when the location of the animal is known to not be on land, *i.e.* a seal at sea cannot be located on land, however extraction of an environmental variable at the GPS location may allocate "land" to the at-sea location. Assuming the error associated with the Kalman smoothed location encompasses an area bordering land and in this case, ice concentration, the weighted mean is able to examine the potential use of the environment around the "land."

Weddell seals in the winter sea ice environment

Figures 7 and 8 present each 20-day MODIS satellite thermal infrared image composite for GPS tagged seals at Dumont d'Urville for 2007 and 2008 respectively. As these are thermal infrared images, the darker areas in the image equate to colder areas indicating heavier ice cover whilst the lighter areas equate to lighter ice cover. For each image,

important sea ice features are noted directly on the image. All Weddell seals remained in the fast ice environment for the entire austral autumn and winter (Fig. 3.7 and Fig. 3.8) The fast ice edge was a consistent northern ice feature in the majority of composite images (*i.e.* Fig. 3.7d – h & Fig. 3.8c - h). Commonwealth Bay (CB) was commonly ice free (*i.e.* Fig. 3.7b – e, 3.7h & 3.8b - h) and the coastal area of Dumont d'Urville (DDU) was often of lower ice concentration relative to the surrounding ice (*i.e.* 3.7a – h & 3.8b – e).

For each 20-day composite, the weighted mean extraction of ice concentration indicated that the seal was occupying a greater range of sea ice concentrations than the direct extraction at each GPS location for the equivalent 20-day period (Table S1 and S2) with one exception – Fig. 3.8e. This exception occurred for the 20-day time period 29/06/2008 – 18/07/2008, which was the heaviest range of ice concentrations the GPS-tagged seals occupied during the austral autumn and winter periods over 2007 and 2008. During this period, ct38w-Delphine-08 was located in ice concentrations between 95 - 100% and ct38w-Aline-Michele-08 was located in ice concentrations between 90 – 100% however for both seals, the dominant ice concentration extracted was between 98 -100% (Table S2).

In general, a wide range in weighted mean ice concentrations (0 – 100%) were extracted for composite time periods up until June in 2008 and 2007. For all composites between 08/06/2008 –16/09/2008, the range in weighted mean ice concentrations was 80% - 100% with no records of concentrations less than 80%. For 2007, high ice concentrations were recorded from 09/06/2007 – 17/09/2007 with a concentration range of 60% - 100% and consequently no records of ice concentration below 60% recorded.

As previously determined, the weighted mean resulted in less locations allocated to land (*i.e.* Fig. 3.7a; Table S1 and Fig. 3.8a; Table S2) and more allocations to mid

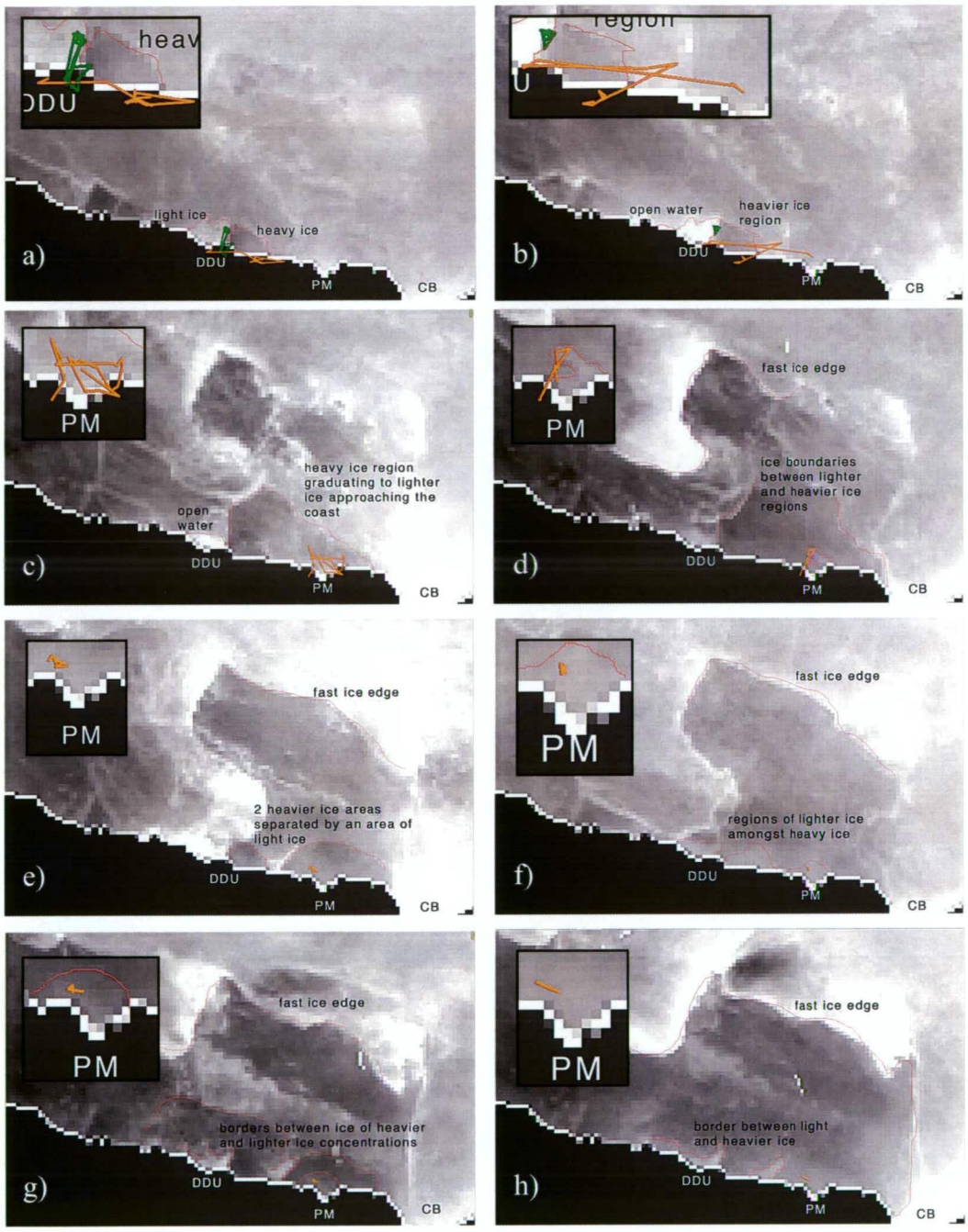


Figure 3.7. High resolution (2km), 20-day composites of thermal infrared MODIS satellite images detailing the ice environment encountered by GPS-tagged Weddell seals at Dumont d'Urville throughout the austral autumn and winter of 2007. Tracks are magnified in each inset within each composite. In each 20-day composite, the green track represents the equivalent 20-day GPS track of wd3-W2-07 and the orange track represent the equivalent 20-day GPS track of wd3-W1-07. wd3-W2-07 stopped transmitting after fig 3.7b. Ice features are noted with text and red lines directly on each composite. 'DDU' = Dumont d'Urville, 'PM' = Port Martin, 'CB' = Commonwealth Bay. 20-day time periods are as follows: **a)** 11/04/2007 – 30/04/2007, **b)** 01/05/2007 – 20/05/2007, **c)** 21/05/2007 – 09/06/2007, **d)** 10/06/2007 – 29/06/2007, **e)** 30/06/2007 – 19/07/2007, **f)** 20/07/2008 – 08/08/2007, **g)** 09/08/2007 – 28/08/2007, **h)** 29/08/2007 – 17/09/2007

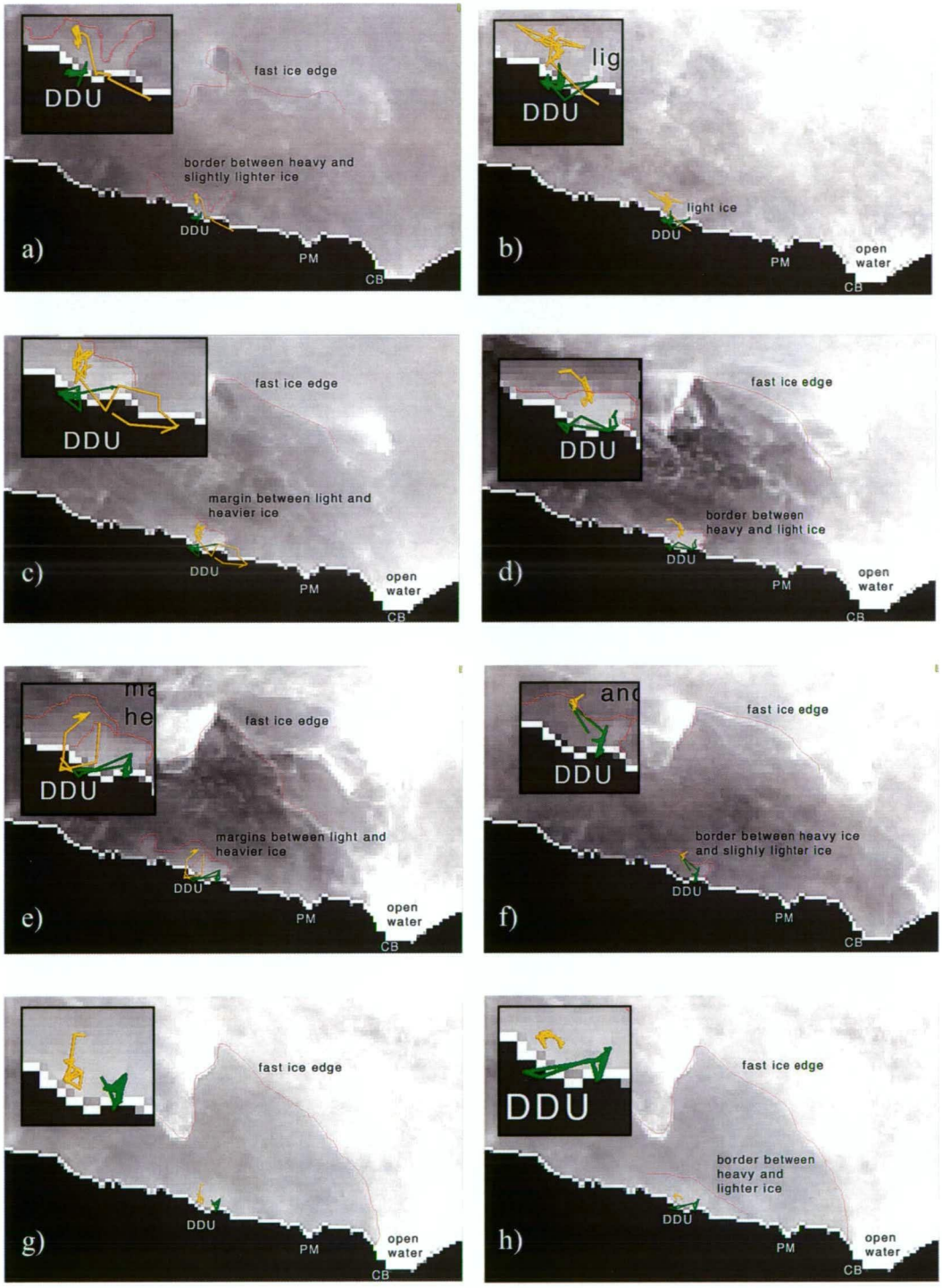


Figure 3.8. High resolution (2km), 20-day composites of thermal infrared MODIS satellite images detailing the ice environment encountered by GPS-tagged Weddell seals at Dumont d'Urville throughout the austral autumn and winter of 2008. Tracks are magnified in each inset within each composite. In each 20-day composite the green track represents the equivalent 20-day GPS track of ct38w-Delphine-08 and the orange track represent the equivalent 20-day GPS track of ct38w-Aline-Michele-08. Ice features are noted with text and red lines directly on each composite. 'DDU' = Dumont d'Urville, 'PM' = Port Martin, 'CB' = Commonwealth Bay. 20-day time periods are as follows: **a)** 10/04/2008 – 29/04/2008, **b)** 30/04/2008 – 19/05/2008, **c)** 20/05/2008 – 08/06/2008, **d)** 09/06/2008 – 28/06/2008, **e)** 29/06/2008 – 18/07/2008, **f)** 19/07/2008 – 07/08/2008, **g)** 08/08/2008 – 27/08/2008, **h)** 28/08/2008 – 16/09/2008.

range concentrations (*i.e.* Fig. 3.7b; Table S1 and Fig. 3.8c; Table S2) as compared to the GPS ice concentration extraction. By comparing the high resolution ice environment in each composite with the weighted mean ice concentrations for the equivalent period, it is clear that the weighted mean is able to provide an understanding of the potential ice environment encountered by the Weddell seals in the absence of high quality locations such as GPS. At times, the weighted mean may provide a more accurate understanding as seen for seal wd3-W2-07 in Figure 3.7b. According to the thermal composite, wd3-W2-07 occupies an area of open water bordering on heavy ice. Potentially this animal has the ability to occupy ice concentrations of both 0% and 100%. The GPS extraction for this period allocates all locations to ice concentrations between 90 – 95% (Table S2). However, the weighted mean indicates the seal occupies a range of ice concentrations between 50 and 100%. Another example occurs in the 20-day thermal composite detailed in Figure 3.7c in which is it apparent that seal wd3-W1-07 had the potential to access the open water occurring deep within Port Martin, adjacent to the coast. Ice concentrations extracted at each GPS location indicated that wd3-W1-07 accesses areas of high ice concentration of 85% and above. For the same 20-day period, the weighted mean extraction also indicates occupation of areas of ice concentration 85% and above however, 0.5% of all locations occur within the 0 – 10% ice concentration (Table S1). Whilst the time spent by wd3-W1-07 in open water was marginal, the weighted mean highlights the potential for this area to be accessed. For the Weddell seals in the winter sea ice environment of Dumont d'Urville in 2007 and 2008, the composites and ice concentration extractions all confirm that these seals occupy a heavy ice environment within the fast ice zone, with lighter ice concentrations and open water accessed occasionally throughout the entire austral autumn and winter.

DISCUSSION

Since the early development of state space models (Jonsen *et al.* 2003), there have been many techniques developed that incorporate location error when describing animal movement (e.g. (Horne *et al.* 2007; Tremblay *et al.* 2009; Patterson *et al.* 2010). These techniques are often used to describe animal movement in detail such as determining areas of restricted search (Bailey *et al.* 2009), estimating home range (Horne *et al.* 2007) and sex-specific movement tactics (Breed *et al.* 2009) for example. Movement patterns are complex however and can be influenced by life history, physiology and the environment (Patterson *et al.* 2008). Therefore these models not only provide the opportunity to describe animal movement, but also begin to disentangle the role of the environment in animal movement. The next step in the development of these models is to assess the various influences on movement such as environmental covariates given the uncertainty surrounding animal locations.

Animal movement is often examined in relation to environmental variables by extracting the relevant environmental information at the raw or filtered location of the animal (Guinet *et al.* 2001; Lea and Dubroca 2003). Environmental data can be retrieved at various resolutions. For example, when extracting bathymetry, it is possible to access publicly available data sets from coarse (ETOPO2 – 2 minutes) through to fine (GEBCO - 30 seconds) resolution. When examining animal movement on a fine scale in relation to environmental covariates, it is important to use the finest resolution data available, as this will best approximate the scales at which predators are making foraging decisions. However, when trying to examine the role of the environment in animal movement, there are a number of limiting factors to consider. Depending on the nature and scale of the questions being asked, these include the resolution of the error associated with each location and the resolution of the environmental data. As

demonstrated in this study, even when using filtered/smoothed data it is possible for the spatial error associated with a location to lead to the matching of incorrect environmental data. In fact, even the small spatial error associated with high quality GPS locations may be enough to result in incorrect extractions of sea ice concentration. This is particularly true when an animal is located in a highly variable environment such as the ice edge – a GPS location that is correct to within 55m of the actual seal location may place the seal in heavy ice when in fact the seal is located in open water directly adjacent to the heavy ice. In this case, the allocation of ice concentration to that location may be as great as 100% when in fact the true concentration is 0%.

All locations used to examine animal movement have some degree of associated error therefore an appropriate approach when extracting environmental information taking into account location uncertainty involves estimating the "error ellipse" around a location. The error ellipse is a representation of an area determined by the probability density associated with a location. All values of the relevant environmental variables can then be extracted within the area defined by the ellipse with their importance weighted using the probability distribution. In this study, we successfully used a weighted mean of ice concentration to produce a data set that was representative of the "real" ice concentration values (as determined by the GPS data set). The weighted mean extraction was also able to take into account presence on land within the "error ellipse" making it a better method for extracting ice concentration for Weddell seal locations at Dumont d'Urville, which are often close to land. When examining the influence of environmental variables on animal behaviour, it may be useful to use not only the weighted mean but also the range and median values of the environmental variable within the "error ellipse." Revisiting the example in which a seal is located at the ice edge on the border between heavy ice and open water with the assumption that the error

ellipse may encompass ice concentrations of around 100% and 0%, it is clear that the weighted mean only partially helps in regard to assigning a correct ice concentration. The weighted mean will in fact give a "blurred" ice concentration value derived from pixels with contrasting ice concentrations, explaining why the weighted mean ice concentrations tended to have higher representation of mid ice concentrations than the GPS locations. Regardless, when examining the ice environment occupied by the Weddell seals throughout 2007 and 2008, the weighted mean was able to provide a clear representation of the ice environment the Weddell seals occupied. Weddell seals occupied heavy ice for much of the austral autumn and winter especially from June onwards, within the fast ice zone. The 20-day thermal infrared composites indicated that on occasion, the seals occupied marginal ice areas between heavy and light ice. The weighted mean extraction provided evidence for this in the distribution of high and low ice concentrations extracted over that period that were not present in the GPS extraction.

For historic data sets that contain Argos locations alone, filtering/smoothing with modern state space models will provide more accurate information to answer spatial questions than raw Argos alone, given the use of an environmental data set at an appropriate resolution. Where possible, assuming the filtered/smoothed data provides an estimate of error associated with each location, extracting environmental information according to the spatial error is the ideal approach. In addition, the increasing use of oceanographic data collected by tagged marine animals (Charrassin *et al.* 2008; Roquet *et al.* 2009) will be incorporated into global databases and oceanographic models in which spatial accuracy is very important. By incorporating estimates of location error, the use of a high resolution environmental data set will only improve the ability to establish the role of the environment in animal behaviour.

Supplementary Material

Table S1. Habitat use of the ice environment by each GPS tagged Weddell seal in each 20-day thermal infrared composite image for 2007 (Figure 3.7). *Date* indicates the 20-day time period each images covers and *seal* indicates the seal ID and corresponding track colour on each 20-day composite in Figure 3.7. Note that wd3-W2-07 ceases transmission by 20-day period starting 21/5/2007. *MODIS thermal infrared composite image* is a qualitative description of the ice environment the seal occupies according to the high resolution composite. As it is not possible to extract ice concentration from these composites, ice was extracted from AMSR-E ice concentration images – the relevant ice concentrations for each 20-day period are shown as percentages in *AMSR-E ice concentration.* The percentage of each ice concentration in the 20-day period as determined by direct extraction at each GPS location is shown in *GPS extraction* whilst the percentage of each ice concentration as determined by the weighted mean is shown in *Weighted mean extraction.*

Date	Seal	MODIS thermal composite image	AMSR-E ice concentration (%)	GPS extraction (%)	Weighted mean extraction (%)
11/04/2007 - 30/04/2007 **Figure 3.7a**	wd3-W1-07 (orange)	Track extremely coastal crossing area of "light ice" adjacent to area of "heavy ice."	20 – 30 40 - 50 60 – 70 85 – 90 90 - 95 95 - 98 98 – 100 land	- - - - - - 95.24 4.76	1.93 0.97 11.59 3.86 3.38 8.21 70.04 -
	wd3-W2-07 (green)	Track coastal and heading north but staying on the edge of the "light ice" area.	20 – 30 30 – 40 60 – 70 80 – 85 85 – 90	- - 17.86 - -	4.84 2.69 13.44 3.76 4.30

			90 - 95 95 – 98 98 - 100	- 7.14 75.0	12.37 6.99 51.61
1/05/2007 - 20/05/2007 **Figure 3.7b**	wd3-W1-07 (orange)	Track spans the "heavier ice region" adjacent to the lighter ice area around Port Martin.	30 – 40 40 – 50 60 – 70 70 - 80 85 – 90 90 - 95 90 – 95 98 - 100	- - - - - 33.33 - 66.67	3.06 3.57 5.10 4.59 2.55 32.65 23.47 25.0
	wd3-W2-07 (green)	Track concentrated around the edge of the open water in the Dumont d'Urville area and borders the adjacent "heavier ice region."	50 – 60 60 - 70 70 – 80 80 – 85 85 - 90 90 – 95 95 – 98 98 - 100	- - - - - 100 -	7.18 0.51 20.0 4.10 4.10 11.79 14.36 37.95
21/05/2007 - 09/06/2007 **Figure 3.7c**	wd3-W1-07 (orange)	Track constrained to the heavy ice region around Port Martin, possibility of accessing open water adjacent to the Port Martin coast.	0 – 10 85 – 90 90 – 95 95 – 98 98 - 100	- 11.54 15.38 30.77 42.31	0.50 5.56 4.04 13.64 76.26
10/06/2007 - 29/06/2007 **Figure 3.7d**	wd3-W1-07 (orange)	Track remains in the Port Martin area following the border between lighter and heavier ice.	85 – 90 90 – 95 95 – 98 98 - 100	- - 72.73 27.27	5.88 33.61 1.68 58.82
30/06/2007 -	wd3-W1-07 (orange)	Track very constrained within homogenous ice in the Port Martin region.	80 – 85 85 – 90	33.33 -	5.49 22.56

19/07/2007 **Figure 3.7e**			90 – 95 95 – 98 98 - 100	- 33.33 33.33	29.27 26.22 16.46
20/07/2007 - 08/08/2007 **Figure 3.7f**	wd3-W1-07 (orange)	Track remains very constrained within homogenous ice in the Port Martin region.	60 – 70 70 – 80 80 – 85 85 – 90 90 – 95 95 - 98 98 - 100	30.77 7.69 23.08 30.77 - - 7.69	19.81 16.04 15.57 23.58 8.49 7.08 9.43
9/08/2007 - 28/08/2007 **Figure 3.7g**	wd3-W1-07 (orange)	Track remains very constrained within heavy homogenous ice in the Port Martin region.	70 – 80 80 – 85 85 - 90 90 – 95 95 – 98 98 - 100	75.0 - - 25.0 - -	2.22 29.44 34.44 24.44 3.89 5.56
29/08/2007 - 17/09/2007 **Figure 3.7h**	wd3-W1-07 (orange)	Track remains in Port Martin region in homogenous ice that appears of lighter ice concentration relative to previous 20-day composite.	70 – 80 80 – 85 85 – 90 90 – 95 95 – 98 98 - 100	- - 0.50 0.50 - -	50.70 27.23 9.86 7.98 3.76 0.47

Table S2. Habitat use of the ice environment by each GPS tagged Weddell seal in each 20-day thermal infrared composite image for 2008 (Figure 3.8). *Date* indicates the 20-day time period each images covers and *seal* indicates the seal ID and corresponding track colour on each 20-day composite in Figure 3.8. *MODIS thermal infrared composite image* is a qualitative description of the ice environment the seal occupies according to the high resolution composite. As it is not possible to extract ice concentration from these composites, ice was extracted from AMSR-E ice concentration images – the relevant ice concentrations for each 20-day period are shown as percentages in *AMSR-E ice concentration.* The percentage of each ice concentration in the 20-day period as determined by direct extraction at each GPS location is shown in *GPS extraction* whilst the percentage of each ice concentration as determined by the weighted mean is shown in *Weighted mean extraction.*

Date	Seal	MODIS thermal composite image	AMSR-E ice concentration (%)	GPS extraction (%)	Weighted mean extraction (%)
10/04/2008 - 29/04/2008 **Figure 3.8a**	ct38w-Delphine-08 (green)	Track very coastal, within fast ice zone and an area of low ice concentration persisting around Dumont d'Urville.	0 - 10 70 – 80 85 – 90 90 – 95 95 – 98 98 – 100 land	- - - - 9.26 11.11 79.62	0.79 2.76 4.72 5.11 8.66 25.20 52.76
	ct38w-Aline-Michele-08 (orange)	Track occurs near the border between lighter and heavier ice within the fast ice zone. Light ice region occurs around Dumont d'Urville.	0 – 10 70 - 80 80 – 90 90 – 95 95 – 98 98 – 100	- - - 5.26 15.79 78.95	1.34 0.34 8.05 0.67 13.76 75.84
30/04/2008 - 19/05/2008 **Figure 3.8b**	ct38w-Delphine-08 (green)	Ice environment is very heterogeneous with no clear ice boundaries however track occurs close to the coast where there is a thin region of heavier ice concentration plus an area of very light ice.	50 – 60 70 - 80 85 – 90 90 – 95 95 - 98	- - - - 3.45	1.70 3.06 0.34 13.27 7.48

			98 - 100 land	15.52 81.03	16.33 57.82
	ct38w-Aline-Michele-08 (orange)	Ice environment is very heterogeneous with no clear ice boundaries, track occurs within an area of fairly uniform ice concentration with northern borders of the track touching on heavy ice concentration.	70 - 80 90 – 95 95 – 98 98 – 100	- 1.75 19.30 78.95	0.93 1.55 24.84 72.67
20/05/2008 - 08/06/2008 **Figure 3.8c**	ct38w-Delphine-08 (green)	Track hugs the coast where a thin vein of heavy ice persists adjacent to the general region of light ice associated with Dumont d'Urville.	30 – 40 40 – 50 50 – 60 90 - 95 95 – 98 98 – 100 land	- - - - 1.72 17.24 81.03	0.32 0.32 3.51 1.60 12.46 30.99 50.80
	ct38w-Aline-Michele-08 (orange)	Track occurs in lighter ice region around Dumont d'Urville with northern edge of the track occurring in higher ice concentrations.	30 – 40 60 – 70 70 - 80 90 – 95 95 – 98 98 – 100	- - - 3.22 22.58 74.19	0.63 1.26 0.63 4.09 19.81 73.58
09/06/2008 - 28/06/2008 **Figure 3.8d**	ct38w-Delphine-08 (green)	Track remains coastal around patches of heavy ice concentration within the general area of lighter ice around Dumont d'Urville.	90 - 95 95 – 98 98 – 100 land	- 10.81 67.57 21.62	10.61 33.33 56.06 -
	ct38w-Aline-Michele-08 (orange)	Track crosses boundary between the lighter ice area of Dumont d'Urville and the bordering heavier ice region.	90 - 95 95 – 98 98 - 100	- 15.0 85.0	1.23 19.67 79.10
29/06/2008 - 18/07/2008	ct38w-Delphine-08 (green)	Track remains very coastal crossing persistent patches of heavy ice close to the continent but also occurring in the lighter ice region around Dumont d'Urville.	95 – 98 98 – 100 land	14.58 68.75 16.67	22.27 77.73 -
	ct38w -	Track occurs in lighter ice region around Dumont d'Urville as well	90 – 95	4.17	-

Figure 3.8e	Aline-Michele-08 (orange)	as crossing into the heavier ice environment.	95 – 98 98 – 100 land	6.25 75.0 14.58	24.69 58.16 17.15
19/07/2008 - 07/08/2008 **Figure 3.8f**	ct38w-Delphine-08 (green)	Ice environment has become quite homogenous with the traditionally lighter ice region around Dumont d'Urville of similar concentration to the surrounding regions. Track however no longer hugs the coast but moves northwards to the boundary between the marginally lighter ice around Dumont d'Urville and the slightly heavier ice to the north of Dumont d'Urville.	80 - 90 85 – 90 90 – 95 95 – 98 98 – 100	- 6.12 34.69 46.94 12.24	7.27 1.92 24.14 41.0 25.67
	ct38w-Aline-Michele-08 (orange)	Track occurs on the border between the marginally lighter ice around Dumont d'Urville and the slightly heavier ice to the north of Dumont d'Urville.	85 – 90 90 – 95 95 – 98 98 – 100	5.26 52.63 18.42 23.68	13.13 41.31 22.39 23.17
08/08/2008 - 27/08/2008 **Figure 3.8g**	ct38w-Delphine-08 (green)	Track constrained to very homogenous ice environment in the Dumont d'Urville region.	80 - 85 85 – 90 90 – 95 95 – 98 98 – 100	- 31.58 31.58 23.68 13.16	0.37 35.32 28.25 24.16 11.90
	ct38w-Aline-Michele-08 (orange)	Track constrained to very homogenous ice environment in the Dumont d'Urville region.	80 - 85 85 – 90 90 – 95 95 – 98 98 - 100	- 20.41 32.65 24.49 22.45	2.25 17.60 41.57 25.47 13.11
28/08/2008 - 16/09/2008 **Figure 3.8h**	ct38w-Delphine-08 (green)	Track constrained to very homogenous ice environment in the Dumont d'Urville region however moves southward to occupy the coastal ice zone again.	80 – 85 85 – 90 90 – 95 95 – 98 98 – 100 land	4.65 30.23 27.91 27.91 4.65 4.65	3.49 29.46 21.32 33.33 5.81 6.59
	ct38w-Aline-	Track constrained to very homogenous ice environment in the	80 – 85	5.0	-

	Michele-08 (orange)	Dumont d'Urville region.	85 – 90 90 – 95 95 – 98 98 - 100	35.0 45.0 5.0 10.0	24.47 49.79 18.14 7.59

4. Winter foraging strategies of Weddell seals – individual variability and the influence of local environmental conditions.

To be submitted as: Andrews-Goff V, Hindell MA, Patterson TA, Field IC, Wheatley KE, Charrassin JB. Winter foraging strategies of Weddell seals – individual variability and the influence of local environmental conditions.

ABSTRACT

Weddell seals are unique amongst the Antarctic ice seals remaining close to the Antarctic continent year-round with no escape from the harsh conditions of the austral winter. Here we investigate the diving behaviour of Weddell seals throughout the austral autumn and winter and how the local winter environment influences diving behaviour. In particular, we quantify the vertical and horizontal movements of 12 Weddell seals using satellite telemetry at two locations – Dumont d'Urville and Davis over 3 years. Each of the seals exhibited a dominant foraging strategy: (i) benthic foragers (n = 5) characterised by dives of intermediate depth (87.08 ± 0.72m) and duration (8.42 ± 0.05 min) over relatively shallow bathymetric depth (147.01 ± 1.04m), (ii) mid water column epipelagic foragers (n = 4) characterised by shallow (70.8 ± 0.45m) and long dives (9.22 ± 0.50 min) over intermediate bathymetric depths (156.96 ± 0.62m) and (iii) upper water column epipelagic foragers (n =3) characterised by short (7.24 ± 0.06 min) but deep dives (104.92 ± 1.16m) over relatively deep bathymetric depths (459.90 ± 2.0m). The benthic foragers concentrated dives over more complex benthos relative to areas with low dive densities; however, bathymetry did not influence the spatial diving distribution of the two epipelagic foraging groups. The degree of individual variability in foraging strategy indicates that even within the one population, responses to changes in the environment will be varied and unpredictable. State space models assigned the behavioural mode "search" to the majority of locations (97.8%) most likely due to the local foraging nature of the seals that moved on average 4.96 ± 0.13km per day. Mixed effects Cox proportional hazards models were able to link diving bout behaviour to environmental variables with the variables *ice concentration*, *wind speed* and *temperature* included in the best model along with *month* ($R^2 = 0.154$). Weddell seal diving bouts were more likely to end when in heavy ice conditions

presumably associated with survival and less likely to end when associated with high wind speeds and low temperatures due to thermoregulatory requirements.

INTRODUCTION

Marine mammals employ foraging strategies that have evolved as a trade off between physiological constraints, functional performance and environmental features (Costa and Gales 2003). Physiological constraints include aerobic dive limit, digestion and thermoregulation (Rosen *et al.* 2007), functional performance includes swim speed (Kooyman 1989), body size (Weise 2010) and locomotor pattern (Williams *et al.* 2000) whilst environmental features include in particular prey distribution which is often related to bathymetry (Burns *et al.* 2008) and/or oceanographic conditions (Bailleul *et al.* 2010).

Marine mammal foraging strategies are commonly classified according to the relative depth at which a seal forages. These range from benthic (diving to the sea floor) versus epipelagic and mesopelagic (midwater diving - hereafter referred to as 'pelagic;' Costa et al. (2004), Villegas-Amtmann *et al.* (2008)). Benthic foraging strategies have the potential to contrast functionally with pelagic foraging strategies as benthic foragers maximise their time at the benthos (Costa *et al.* 2004). If this benthos occurs in deep water, benthic foragers will be required to operate at their maximum physiological capacity.

Marine mammals may exhibit a dominant foraging strategy which can be related to a geographic region or habitat, sex or age group (Villegas-Amtmann *et al.* 2008). For example, Antarctic fur seals at the Kerguelen archipelago dive deeply and feed primarily on myctophids (Lea *et al.* 2002; Lea *et al.* 2008) whilst Antarctic fur seals at South Georgia are shallow diving and feed predominantly on krill (Croxall *et al.* 1985). Male southern elephant seals forage benthically on the Antarctic continental shelf whilst

females switch from benthic foraging to pelagic foraging as they move north with the ice edge (Bailleul *et al.* 2007).

The Weddell seal is unique amongst pinnipeds – it is the most southerly occurring with a circumpolar distribution (Lugg 1966) year round (Kooyman 1981). The limited information available on the winter movements of Weddell seals suggests they are closely associated with the fast and pack ice (Testa (1994), Chapters 2 and 3) and observations of Weddell seals north of the Antarctic convergence are few (Kooyman 1981). As such, the Weddell seal is effectively constrained to the Antarctic continental shelf and has no option but to function within the winter ice environment under harsh weather conditions. Weddell seals exhibit reductions in foraging success and survival due to climate mediated environmental conditions and their consequent effects to prey availability (Hadley *et al.* 2007b; Proffitt *et al.* 2007). However, little is known of how the local winter environment, such as ice concentration and weather conditions influence the behaviour of Weddell seals apart from a single study implicating local environmental conditions in reduced reproductive success for Weddell seals at the Vestfold Hills (Lake *et al.* 2008).

Studies examining the role the environment plays on foraging have had varied success with many finding significant relationships but having low explanatory power. Individual variability can make it difficult to detect an animal-environment relationship especially as seals respond to the environment at scales that are finer than can be measured with remote sensing of the environment. For example, Bradshaw *et al.* (2004) used a complex, non-linear model and found that sea surface temperature and sea surface gradient predicted a significant but relatively small (4%) proportion of time spent at sea for female southern elephant seals. Similarly, Guinet *et al.* (2001), using a simpler multi linear regression analysis found that the amount of time spent diving in an

area was related to distance from the colony, bathymetry and bathymetric gradient, surface chlorophyll concentration and gradient and sea surface temperature and gradient, although again the total variance explained was low (2%) when examining the influence of these variables on a fine spatial scale (0.1°×0.1°). However, this increased to 44% at a coarser spatial scale (2°×2°). More recently, Bailleul *et al.* (2010) found that within cyclonic eddies, seals dive deeper with higher sea level anomaly values during intensive foraging phases - the total variance explained by the linear mixed effects model was 2%. Therefore, whilst models are useful in explaining the variation in foraging behaviour of marine mammals, their predictive capacity is both variable and limited (Bradshaw *et al.* 2004).

Under certain circumstances, alternative analytical approaches may offer a better approach to examining the influence of the environment on animal behaviour, such as 'time to event' models including the Cox proportional hazards model (Cox 1972). Examples of its use outside medical research, where it is used to assess survival times, include investigating patch leaving tendency (Wajnberg *et al.* 2003) and identifying and investigating environmental variables that influence first passage time (Freitas *et al.* 2008c). Freitas *et al.* (2008c) applied Cox proportional hazards models to the habitat use of three species, ringed seals *Phoca hispida*, white whales *Delphinapterus leucas* and male Atlantic walruses *Odobenus rosmarus rosmarus* (Freitas *et al.* 2009). The approach enabled: i) identification of environmental variables that best helped to explain time spent in an area, ii) measurement of the animal's response to those environmental conditions and, iii) a prediction of habitat use. These models also provide a measure of variability that is attributable to the individual. For example, for male Atlantic walruses during the non-breeding season, the environmental variables bathymetric depth and distance from shore influenced first passage time. The walruses

responded to these environmental variables through an increased risk of leaving an area with increasing depth and at increased distances from the shore. Specifically, the odds of leaving an area were 2.6 times higher in deep versus shallow waters and 9 times higher at distances further from the shore as compared to distances close to the shore. The per-individual variability of leaving an area was 2.2 times higher or smaller than the overall probability. Compared to the models outlined earlier, the Cox proportional hazards models explained a much higher proportion of the variability explaining between 27.5% and 57.1% of the variability for these three species.

In this study, we aim to describe the general diving behaviour of Weddell seals during the austral autumn and winter, examining foraging strategies of individuals, general movement patterns and determining the influence of the environment on diving behaviour using mixed effects Cox proportional hazards models.

METHODS

Capture, handling and tag deployment

A total of 20 adult, post-moult, female Weddell seals were captured at two locations: Dumont d'Urville – 66°40' S, 140°00 E, and the Vestfold Hills - 68°33' S, 78°15' E. Animal handling occurred over three successive summers: 2006 (Dumont d'Urville: n = 5, Vestfold Hills: n = 5), 2007 (n: Dumont d'Urville = 3, n: Vestfold Hills = 3), 2008 (n = 5; Dumont d'Urville only). Each seal was equipped with a satellite relay data logger (SRDL) with conductivity, temperature and depth function (Sea Mammal Research Unit, University of St. Andrews, Scotland). The seals were approached on the ice by foot and temporarily restrained with a head bag or pole net and an intravenous injection of zoletil (1:1 mixture of tiletamine and zolazepam) at a dosage of 0.5mg/kg (Wheatley

et al. 2006a) administered. The SRDL was then attached to the head with the antenna facing foreword using a two component industrial epoxy. The seal was observed during recovery from anaesthesia and allowed to enter the water when no longer sedated. For the purposes of this paper, only 12 seals (n = 6 at Dumont d'Urville and n = 6 at the Vestfold Hills) had sufficient data spanning the austral autumn and winter to be included in analyses.

The SRDLs were programmed to record dive depth, dive start time, dive duration and post-dive surface interval every 4s. The tags also recorded the start and end time of each haul-out. For each 6h period, the tags also recorded a time-line summary of the percent time that the animal spent hauled out, diving and cruising. The tag recognised a haulout when it had been dry for 10 min and the haulout ended when the tag was wet for 40s. During haulout, the tag attempted to uplink to overhead satellites every 1min 20s for the first 5h and then cycled off for 6h and on for 1h. At all other times, the tag attempted to uplink every 40s.

Foraging strategies

Foraging strategies were examined in three ways:

1) A cluster analysis was used to identify predominate dive types – benthic, mid water column or upper water column to determine each individuals use of the water column.
2) Areas of high use were determined using 2-dimensional and 3-dimensional kernel density maps to examine individual use at the surface and at depth.
3) Behavioural states were assigned to individual tracks using a state space model to differentiate for each individual areas used for "transit" from areas used for "search" behaviour.

Cluster analyses

Each dive was classed as *benthic*, *mid water column* or *upper water column* by comparing maximum dive depth to the weighted mean of bathymetry at the Kalman smoothed dive location (see chapter 3). These Kalman smoothed locations were Argos locations that have been filtered using a combination of heuristic speed filtering and a state-space approach employing the Kalman filter and smoother (full details of the method are given in Patterson *et al.*(2010)). The Kalman filter/smoother takes into account Argos location error and provides information on the error distribution associated with each Kalman smoothed location. The Kalman filter does not assign behavioural states such as "transit" and "search." The estimated error distribution of each Kalman smoothed location can then be used to produce a weighted mean of any environmental information extracted at the site of each Kalman smoothed location.

Conventional methods of dive classification for marine predators classify dives according to depth – benthic dives occur at the benthos (as classified for rockhopper penguins (Tremblay and Cherel 2000)), epipelagic dives occur between 0-200m (as classified for leatherback turtles (Hays *et al.* 2006)) and mesopelagic dives occur between 200 - 1000m (as classified for sperm whales (Watwood *et al.* 2006)). For the Weddell seals in this study, 89% of all dives occured between 0 – 200m, encompassing the benthic and epipelagic classifications and 95% of all dives were less than 300m encompassing the benthic, epipelagic and mesopelagic classifications. As the majority of pelagic dives would therefore fall within the epipelagic class, we chose to instead class dives according to their position in the water column, thereby attempting to detect any foraging strategies within the epipelagic zone and include information on the depth actually available to the diving seal. Therefore, a dive was classified as *benthic* if it occurred within 10% of the bottom of the water column, *upper water column* if it

occurred in the top 30% of the water column and *mid water column* for those depths in between (30% - 90%). Proportion of dives in each category was determined on a daily basis for each individual and a cluster analysis run on these daily summaries (n = 1870) to produce three clusters or groups of behaviour. Use of the water column could then be summarised per individual for the entire tracking period by determining the number of days occurring in each of the three clusters derived, *i.e.* for the entire tracking period, seal awru1-A-06 had X% of days in cluster group 1, Y% of days in cluster group 2 and Z% of days in cluster group 3. An additional cluster analysis was then performed on this overall summary (n = 12) to allocate a single cluster to each individual summarising overall daily use of the water column, i.e. seal awruA-1-06 was allocated to cluster 1. Cluster analyses were run in the R package (R Development Core Team; package *stats*, function *hclust*, method = *ward*) distributed under the GNU general license (www.r-project.org).

Areas of high use – two dimensional

To identify the areas of high use for animals using each foraging strategy, 2-dimensional kernel density maps were constructed on the Kalman smoothed locations. Kernel density methods estimate the (normal) probability density function of spatial and depth variables. Quantiles of kernel density, which are a measure of each raster cell's "place" in a cumulative distribution function, were also calculated and allow standardised comparison between individuals and sites. To examine the bathymetric features of areas of high kernel density versus low kernel density, a $10km^2$ grid was applied to each kernel density map. All bathymetry within each grid square was extracted along with the mean quantile density for that grid square. The average depth, standard error of depth, kurtosis and skewness of each grid cell were then compared

between high use and low use areas. High use was defined as the upper 10% of quantile values whilst low use was defined as the lower 10% of quantile values. Skewness, which quantifies the departure from symmetry (Sokal and Rohlf 1969), gives an indicator of the presence of seamounts and troughs. If the skew is negative, the area contains few "shallow" depths relative to the dominant "deeper" depths, *i.e.* sea mounts. If the skew is positive, the area contains few "deeper" depths relative to the dominant "shallow" depths, *i.e.* troughs. Kurtosis indicates if there are extreme values of bathymetric depth in the high use areas (Sokal & Rohlf 1969). A negative kurtosis indicates widely varied depths whilst a positive kurtosis indicates predominantly uniform depths or a mostly flat area of bathymetry.

To examine the influence of these bathymetric features on habitat use, we constructed a series of linear mixed effects models with the variables *mean bathymetric depth*, *standard error of bathymetric depth*, *bathymetric kurtosis* and *bathymetric skewness* modelled against the binomial term describing *high use* or *low use* grid cells. These models examined each variable separately, including *site* as a random term and incorporated a binomial family structure with a logit link. For *upper water column* (cluster group 3), it was not necessary to include *site* as a random term as there was only one site represented in the data. In this case these variables were modelled against the binomial *use* variable with a generalised linear model again including a binomial family structure with a logit link. All models were run in the R package (linear mixed effects models: library *lme4*, function *lmer*; generalised linear model: library *stats*, function *glm*).

Areas of high use – three dimensional

To construct 3-dimensional kernel density maps, it was first necessary to manipulate the data so that each track also contained information on each dive. SMRU-SRDLs summarise each dive by providing one dive location and four depth-time inflection points where the trajectory changes most rapidly (Fedak *et al.* 2002). These four inflection points do not have a corresponding geographic location. Therefore, we interpolated the location of each inflection depth by matching the time of the location to the Kalman filtered track used for the 2-dimensional kernel density maps resulting in a data set that had a location for each of the four depth inflections within a dive. The kernel density was then run on three dimensions- latitude, longitude and depth. A 3-dimensional isosurface representing the volume of all densities within the 95^{th} quantile was also constructed.

Behavioural states – "search" and "transit"

To quantify habitat use behaviourally, we assigned behavioural state using state space models developed by Jonsen *et al.* (2003). These state space models are time-series models that use observed data to infer "states" to unobservable data and like the Kalman filter, account for the error associated with imprecise locations (Jonsen *et al.* 2003). Unlike the Kalman filter, these state-space models do not provide information on the error distribution at each smoothed location. State space models were fitted to the raw Argos data to retain information on Argos location error used by the models. These models, discussed in detail by Jonsen *et al.* (2003), classify movements as either "search" or "transit" using information on direction, speed and turning angle. A time step of 6h was used.

Influence of environmental variables on dive behaviour

The Weddell seals at Dumont d'Urville and the Vestfold Hills do not return to a central haulout site, rather they hauled out regularly, adjacent to diving bouts, presumably on any stable platform available (see chapter 2). Therefore, we extracted the inter-haulout diving bouts and treated these as individual 'trips.'

For each inter-haulout diving bout location (n = 1025), we derived *average sea ice concentration* (weighted mean), *dominant wind direction, average wind speed, dominant direction of travel (bearing), air temperature* and *average bathymetric depth* (weighted mean). Weather data were sourced from the Australian Government Bureau of Meteorology and were collected for Davis (Vestfold Hills) and Dumont d'Urville station. For all seals and years, the average maximum distance travelled from the base was 98.39 ± 34.47km at Davis and 71.57 ± 7.77km at Dumont d'Urville, so we assumed that the weather at the stations will have been similar to that experienced by the seals. Ice concentration was extracted at all dive and at-sea locations provided by Argos within each diving bout from the daily remote sensing sea ice concentration maps (6.25km grid resolution) retrieved from the Advanced Microwave Scanning Radiometer-Earth Observing System (AMSR-E; Institut fur Umweltphysik Universitat Bremen, http://iup.physik.unibremen.de:8084/amsr/amsre.html). Bearings between subsequent locations within each foraging bout were calculated and then the dominant direction of travel within the bout determined. Bathymetry was extracted from the GEBCO 30s bathymetric grid http://www.gebco.net. For both ice concentration and bathymetric depth, we extracted a weighted mean by weighting each point in the environmental data set by the associated error ellipse from the Kalman smoothed location (see chapter 3).

In order to determine how environmental variables influenced these diving bouts, we modelled diving bout duration as a function of the fixed variables: *ice concentration, wind speed, wind direction, temperature, bearing* and *bathymetric depth* with a mixed effects Cox proportional hazards model (CPH models; Cox (1972)). As CPH models model 'time to event data,' diving bout duration can be likened to time spent in a 'patch.' These models therefore are essentially modelling 'patch leaving tendencies' or the tendency for a diving bout to end. We included *seal* individual as a random effect nested within *site* (Dumont d'Urville or Vestfold Hills). The Cox proportional hazards model is ideal for assessing the nature and magnitude of any effect the environmental variables may have had on diving bouts.

The CPH model is:

$$h(t) = \exp(\beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \ldots + \beta_p X_p) h_0(t)$$

where h(t) is the hazard function – the risk that an animal ends a diving bout at time t. $X_1 + X_2 + X_3 + \ldots + X_p$ are the explanatory variables in the model, whilst $\beta_1 + \beta_2 + \beta_3 + \ldots + \beta_p$ are the coefficients that describe the contribution of these variables. $h_0(t)$ is the baseline hazard function at time t – the risk of a diving bout ending when all continuous explanatory variables are 0 or a pre-defined base value (categorical variable). A random effect term, (b), was added to the model to account for the variability of individual nested within site (Pankratz *et al.* 2005) where b is the per-subject random effects assumed to be normally distributed with a mean of 0:

$$h(t) = \exp(\beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \ldots + \beta_p X_p + b) h_0(t)$$

The CPH model without the random effects term only addresses fixed effects and as such is a 'fixed effects CPH model.' The CPH model with the random effect term added is a 'mixed effects CPH model.'

For both fixed and mixed effects CPH models, the unknown parameters in the model β and *b* coefficients are estimated using maximum likelihood (see Collett 2003; Pankratz *et al.* 2005). The baseline hazard function $h_0(t)$ is estimated from the β coefficients and hazard ratios can be calculated from the exponential of β, e^{β}, and used to extract information on the effects of the covariates (Collett 2003). A hazard ratio above 1 indicates increased risk of a diving bout ending whilst a hazard ratio less than 1 indicates decreased risk of a diving bout ending. A continuous *X* variable with a hazard ratio of 0.8 indicates that the risk of a diving bout ending is 0.8 times or 20% less with each increase in the *X* variable by a predefined unit of *X*. For example, for the continuous variable temperature predefined to be structured in 2°C units, there is 20% less risk of a diving bout ending with each 2°C increase in temperature. A categorical *X* variable (with two or more levels, the first level is baseline) with a hazard ratio of 1.5 indicates that when the *X* variable assumes that level, the risk of the diving bout ending is 1.5 times than when *X* assumes the baseline level. In other words, if ice concentration is classed as 'low', 'medium' and 'high' and 'low' is assigned as the baseline, the risk of a diving bout ending is 1.5 times higher in 'high' concentrations in relation to the baseline level, 'low' concentrations.

All possible additive combinations of the environmental variables were used during the model selection process resulting in 158 models. Wind speed and temperature are known to have an effect on haulout behaviour (Andrews-Goff *et al.* 2010) so the interaction between wind speed and temperature was also included. Selection between each of the 158 candidate models was undertaken using Akaike's

Information Criterion (AIC) corrected to the effective sample size (AIC_c) which was appropriate as the ratio of sample size to the parameters included in the models was small (Burnham & Anderson 2002):

$$AIC_c = -2\log(L) + 2k + \frac{2k(k+1)}{n-k-1},$$

where n is the sample size, in this case log(L) is the penalised log likelihood and k are penalised degrees of freedom (see Pankratz *et al.* 2005). Coefficients of determination (R^2) were calculated using the penalised log likelihoods. The scaled Schoenfeld Residuals were examined for the fixed models (as this was not possible for the mixed effects models) and all variables used were deemed satisfactory. CPH models were fitted using the R package (libraries *survival* and *kinship*). Further detail on fixed and mixed effects CPH models and how to relate them to habitat use can be found in Freitas et al (2008a; 2008b; 2008c; 2009).

RESULTS

Foraging strategies

Predominate dive types - use of the water column

Cluster analyses of daily dive type summaries (proportion of benthic, mid water column, and upper water column dives per day) per individual produced three clear groups or clusters (Fig. 4.1) corresponding to predominantly benthic (Group 2), mid water column (Group 1) or upper water column daily dive behaviour (Group 3; Table 4.1).

Table 4.1: Mean values for each variable used in the cluster analysis. Groups defined by the cluster analysis of daily summaries of dive type (benthic, mid water column, upper water column) with Group 1 dominated by mid water column dives, Group 2 dominated by benthic dives and Group 3 dominated by upper water column dives.

Variable	Group 1	Group 2	Group 3
Percentage of benthic dives	11.12 ± 0.55	65.88 ± 0.79	3.86 ± 0.31
Percentage of mid water column dives	58.19 ± 0.79	11.52 ± 0.41	14.17 ± 0.52
Percentage of upper water column dives	30.63 ± 0.72	22.60 ± 0.73	81.97 ± 0.57

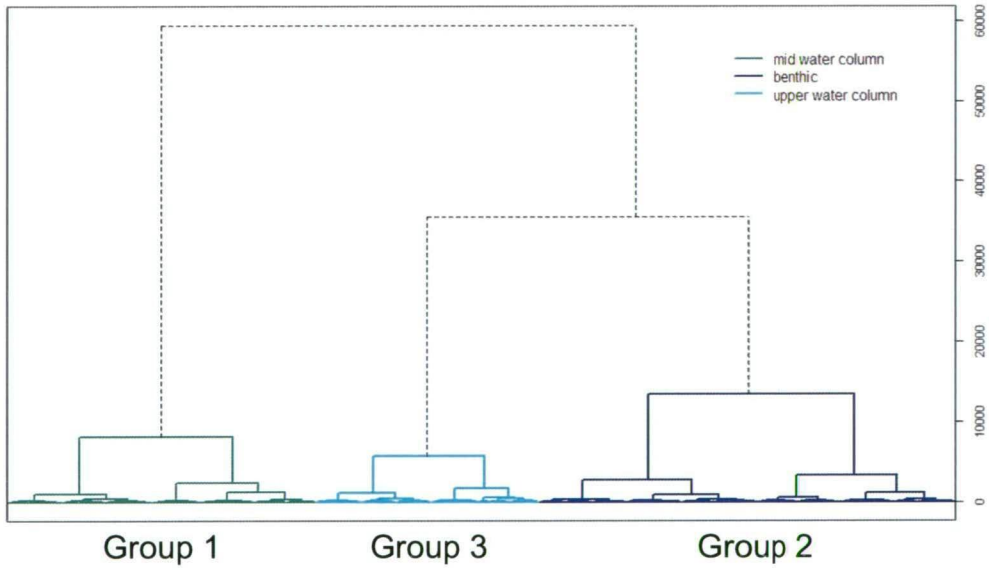


Figure 4.1: Cluster dendogram of cluster analysis performed on daily summaries of dive types (proportion of benthic, upper water column and lower water column dives per day) for all 12 seals demonstrating three clear groups colour coded by their dominant daily dive behaviour - see colour legend top right hand side.

For each tracking day for each seal, one of the three cluster groups (Fig. 4.1) was assigned. For each seal, each cluster group was assigned at varying frequencies however; a dominant group could be detected by examining the cluster group occurring at the highest frequency (Table 4.2). Seal wd3-CTD1-07 was the exception in that it had similar percentages of days classified to Group 1 (benthic) and Group 2 (mid water

column). There was no obvious temporal pattern in days assigned to each group amongst the seals (Fig. 4.2).

Table 4.2: Percentage of days throughout the tracking period assigned to each cluster group defined in Table 4.1 for each individual seal. All seals except wd3-CTD1-07 can be assigned a dominant dive behaviour (benthic, mid water column, upper water column) according to the cluster group with the highest frequency.

Seal ID	Benthic	Mid water column	Upper water column	Final cluster group
ct38w-Denise-08	59.04	20.74	20.21	2 - *benthic*
ct38w-Mathilde-08	63.29	23.19	13.53	2 - *benthic*
ct38w-QueenEliz-08	32.78	51.11	16.11	1 – *mid water column*
wd3-CTD1-07	45.32	43.84	10.84	1 – *mid water column*
wd3-CTD2-07	67.08	19.25	13.66	2 - *benthic*
wd3-CTD3-07	68.05	8.28	23.67	2 - *benthic*
awru1-A-06	27.52	53.21	19.27	1 – *mid water column*
awru1-B-06	7.45	66.49	26.06	1 – *mid water column*
awru1-C-06	61.81	19.44	18.75	2 - *benthic*
wd1-10183-06	17.28	32.10	50.62	3 – *upper water column*
wd1-10213-06	37.06	20.59	42.35	3 – *upper water column*
wd1-10217-06	1.43	28.57	70.00	3 – *upper water column*

The subsequent cluster analysis performed on the overall summary of dive behaviour for the tracking period (Table 4.2) grouped seals in accordance with the dominant dive behaviour described in Table 4.2. For wd3-CTD1-07, a dominant dive behaviour cannot be determined from Table 4.2 but the cluster analysis assigned it to the group defined by predominantly mid water column diving (Fig. 4.3). As can be seen in Table 4.3, this is because the overall diving behaviour of wd3-CTD1-07 is more similar to Group 1 (mid water column) than it is to Group 2 (benthic). The last column

of Table 4.3 presents the cluster group assigned to each seal in this final cluster analysis.

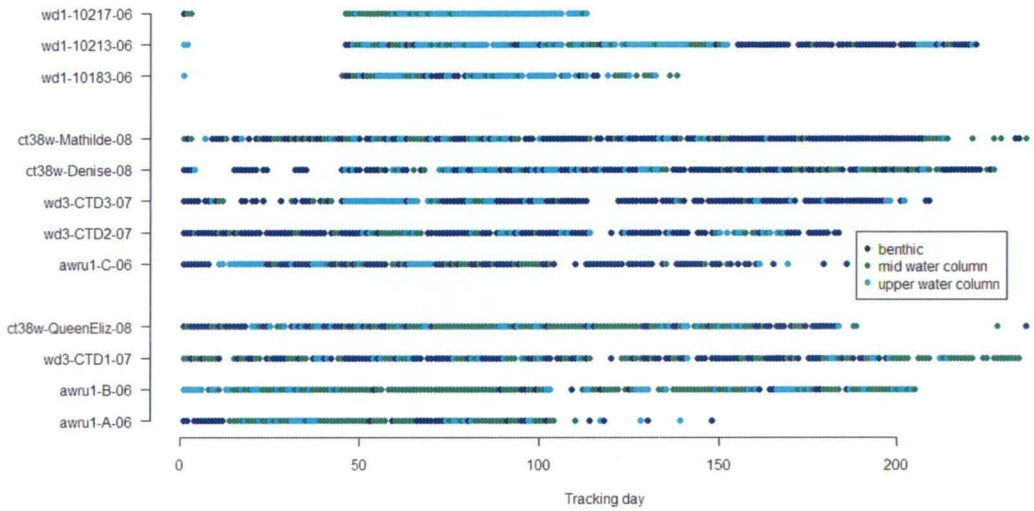


Figure 4.2. Daily allocations of each group derived from the cluster analysis on the proportion of benthic, mid water column and upper water column dives for each day and each seal. The x-axis shows tracking day (number of days since tag deployed) and the y-axis represents each individual seal. Each colour corresponds to a different class of dive behaviour: navy blue: *benthic* (Group 1), green: *mid water column* (Group 2), cyan: *upper water column* (Group 3). The gap in data for the top 3 seals is due to an issue with data collection – for reasons unknown, dive information only was not transmitted throughout this period however diagnostic and summary data were transmitted indicating that tags were functioning.

Table 4.3: Groups derived from the final cluster analysis on overall summary of dive behaviour for the tracking period (Table 4.2). Group 1 is dominated by *mid water column* dive behaviour, Group 2 is dominated by *benthic* dive behaviour and Group 3 is dominated by *upper water column* diving behaviour.

Variable	Group 1	Group 2	Group 3
Percentage of benthic behaviour	28.27 ± 0.79	63.85 ± 0.17	18.59 ± 1.03
Percentage of mid water column behaviour	53.66 ± 0.47	18.18 ± 0.26	27.09 ± 0.34
Percentage of upper water column behaviour	18.07 ± 0.32	17.96 ± 0.20	54.32 ± 0.82

The 12 seals provided data for periods ranging from 116 to 260 days (deployment details in Table 4.4) with a mean of 4443.67 ± 279.97 dives per seal (total of 53, 204 dives). The mean dive depth for individual seals ranged from 53.2m to 156.1m however, overall average dive depth was 93.35m ± 0.45m. Of the *Group 2 – benthic* divers, the majority were individuals from Dumont d'Urville with just one seal from the Vestfold Hills (Fig. 4.3). *Group 3 – upper water column* was made up entirely of individuals tagged at the Vestfold Hills in 2006 (Fig. 4.3). *Group 1 – mid water column* was a mix of seals from both locations with two individuals from Dumont d'Urville and two individuals from the Vestfold Hills (Fig. 4.3).

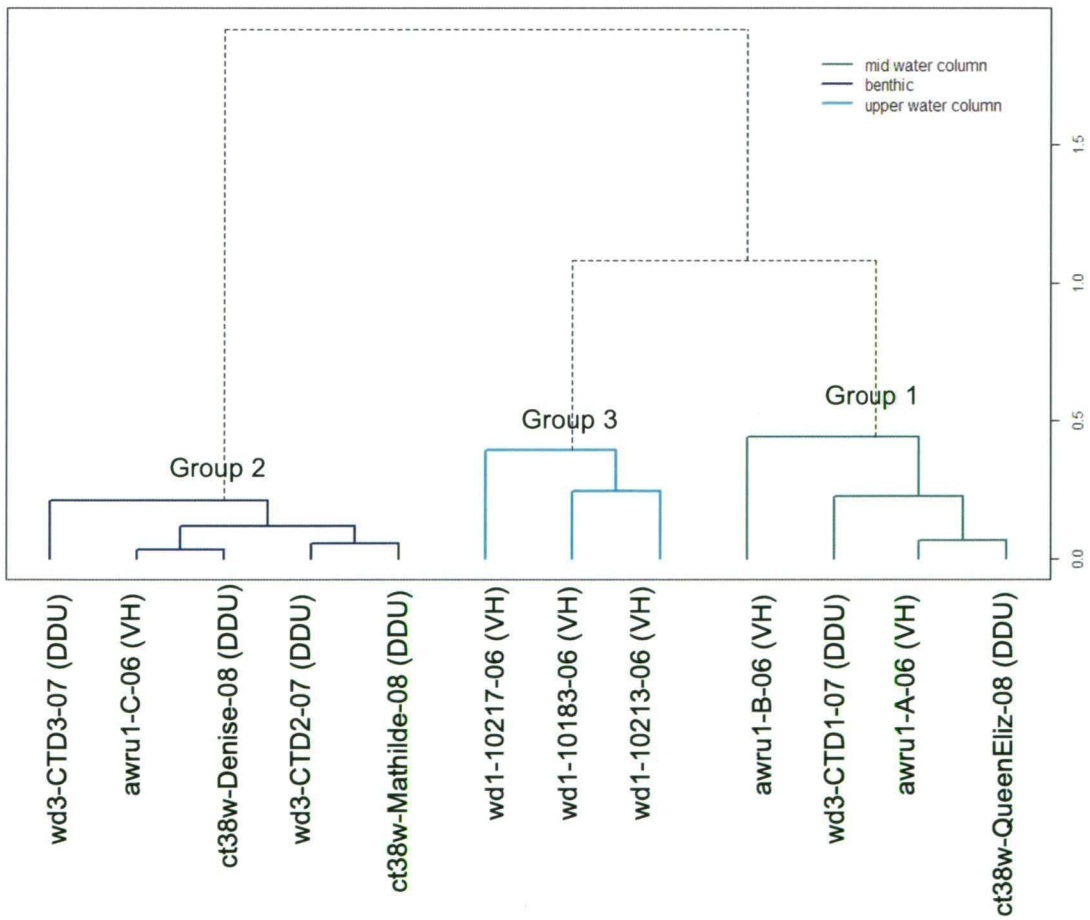


Figure 4.3. Cluster analysis on individual summaries of the proportion of benthic, pelagic and surface dive behaviour for the tracking period producing three distinct groups. Seal ID and location (DDU = Dumont d'Urville, VH = Vestfold Hills) provided at base of tree.

Table 4.4: Summary of deployment for the 12 seals included in this study detailing location of deployment (DDU = Dumont d'Urville; VH = Vestfold Hills), date of deployment, date of last uplink and deployment duration.

Seal ID	Location	Date of deployment	Last uplink	Duration of deployment (days)
ct38w-Denise-08	DDU	22/2/2008	2/11/2008	254
ct38w-Mathilde-08	DDU	21/2/2008	18/10/2008	240
ct38w-QueenEliz-08	DDU	21/02/2008	22/8/2008	183
wd3-CTD1-07	DDU	20/2/2007	7/11/2007	260
wd3-CTD2-07	DDU	20/2/2007	21/8/2007	182
wd3-CTD3-07	DDU	21/2/2007	20/9/2007	211
awru1-A-06	VH	1/3/2007	29/7/2007	150
awru1-B-06	VH	1/3/2007	2/10/2007	215
awru1-C-06	VH	1/3/2007	11/8/2007	163
wd1-10183-06	VH	17/2/2006	9/7/2006	142
wd1-10213-06	VH	16/2/2006	8/10/2006	234
wd1-10217-06	VH	17/2/2006	13/6/2006	116

The mean dive depth for the *Group 1 – mid water column* was shallowest of all groups at 70.80m ± 0.45m whilst the mean dive duration was longest for all groups at 9.22 ± 0.05 minutes (Table 4.5). The mean dive depth for *Group 2- benthic* was deeper than *Group 1 – mid water column* at 87.08 ± 0.72m, however the mean dive duration was shorter at 8.42 ± 0.05 minutes. The mean dive depth for the seals in *Group 3 – upper water column* was much deeper than both *Group 1* and *Group 2* at 104.92 ± 1.16m. Dives were shortest in duration for *Group 3 – upper water column* at 7.24 ± 0.06 minutes. The general trend in dive duration and depth for each group is shown in Figure 4.4.

The percentage of time spent diving per day was greatest for *Group 3 – upper water column* at 49.39 ± 0.83%, intermediate for *Group 2 – benthic* at 44.89 ± 0.60% and least for *Group 1- mid water column* at 43.03 ± 0.64%. Percent time spent at the surface is similar for all groups with *Group 1 – mid water column* spending slightly more time at the surface, 35.35 ± 0.67%, than *Group 3 – upper water column*, 35.20 ±

0.78%. *Group 2 – benthic* spent the least amount of time at the surface at 32.89 ± 0.63%.

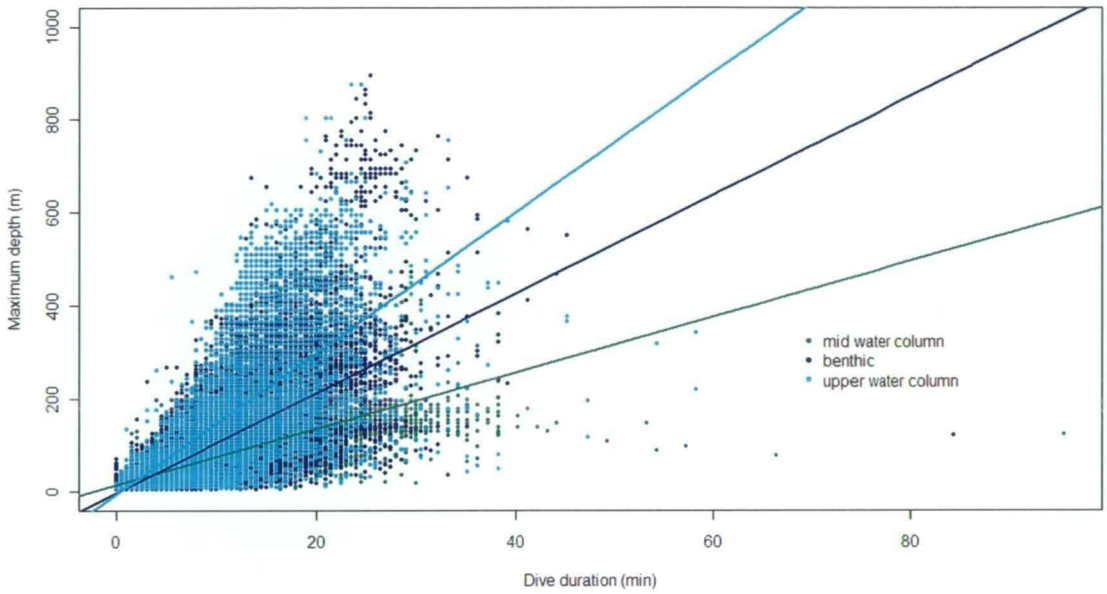


Figure 4.4: Maximum dive depth in metres versus dive duration in minutes colour coded for each cluster group as shown in the colour legend. Dives were longest but shallowest for *Group 1 – mid water column*, intermediate in depth and duration for *Group 2 – benthic* and deepest but shortest for *Group 3 – upper water column*.

The seals in *Group 1 – mid water column* were the shallowest but longest divers diving over a relatively intermediate mean bathymetric depth of 156.96 ± 0.62m. The *Group 2 – benthic* seals were diving at intermediate depths and durations and over a relatively shallow mean bathymetric depth at 147.01 ± 1.04m. *Group 3 – upper water column* were the deepest but shortest divers diving over the relatively deepest bathymetric depths with a mean of 459.90 ± 2.0m.

Assuming a theoretical aerobic dive limit (ADL) of 19.1 minutes for an adult Weddell seal weighing 450 kg (Ponganis *et al.* 1993), for *Group 1 – mid water column*, 7.32% of all dives exceeded the aerobic dive limit. For *Group 2 – benthic*,

Table 4.5: Summary of diving behaviour for the 12 seals included in this study including dive depth, duration, frequency (mean ± se and range) and deployment site (DDU = Dumont d'Urville; VH = Vestfold Hills). Group refers to the group allocated to each individual from the cluster analysis on dive behaviour. Group 1 = mid water column; Group 2 = benthic; Group 3 = upper water column.

Ref	Group	Site	Depth		Duration		Frequency (per day)		
			Mean	Range	Mean	Range	Mean	Range	% time spent diving
awru1-A-06	1	VH	81.1 ± 1.0	4.0 – 282.0	8.6 ± 0.1	< 0.5 - 40.3	37.7 ± 1.4	10 - 86	39.73 ± 1.30
awru1-B-06	1	VH	87.4 ± 0.8	4.0 – 242.0	11.4 ± 0.1	< 0.5 - 66.3	27.2 ± 1.0	0 - 81	43.78 ± 0.95
wd3-CTD1-07	1	DDU	68.7 ± 0.8	5.0 - 583.8	11.0 ± 0.1	< 0.5 - 95.3	22.3 ± 0.9	0 - 71	43.69 ± 1.45
ct38w-QueenEliz-08	1	DDU	63.5 ± 0.9	5.0 - 523.8	8.0 ± 0.1	< 0.5 - 36.3	23.9 ± 1.0	0 - 59	43.90 ± 1.40
awru1-C-06	2	VH	53.2 ± 0.5	4.0 – 202.0	8.6 ± 0.1	< 0.5 - 32.3	28.9 ± 1.6	0 - 98	46.05 ± 1.13
wd3-CTD2-07	2	DDU	124.7 ± 1.4	5.0 - 603.8	9.8 ± 0.1	< 0.5 - 38.3	28.4 ± 1.4	0 - 81	46.27 ± 1.31
wd3-CTD3-07	2	DDU	150.5 ± 2.6	5.0 - 903.8	10.0 ± 0.1	< 0.5 - 44.3	20.8 ± 1.0	0 - 65	43.32 ± 1.12
ct38w-Denise-08	2	DDU	66.3 ± 1.1	5.0 - 543.8	8.9 ± 0.1	< 0.5 - 39.3	20.6 ± 0.9	0 - 71	42.14 ± 1.60
ct38w-Mathilde-08	2	DDU	89.2 ± 1.7	5.0 - 803.8	9.5 ± 0.1	< 0.5 - 84.3	19.5 ± 1.0	0 - 84	47.48 ± 1.40
wd1-10183-06	3	VH	70.2 ± 1.5	6.0 - 316.5	7.0 ± 0.1	< 0.5 - 34.3	24.1 ± 1.9	0 - 85	46.84 ± 1.44
wd1-10213-06	3	VH	156.1 ± 2.2	6.0 - 874.5	9.6 ± 0.1	< 0.5 - 58.3	50.0 ± 1.9	2 - 107	53.72 ± 1.27
wd1-10217-06	3	VH	93.2 ± 2.1	6.0 - 604.5	8.2 ± 0.1	< 0.5 - 35.3	40.0 ± 2.3	0 - 105	43.46 ± 1.34

6.98% of all dives exceeded the aerobic dive limit and for *Group 3 – upper water column,* 6.71% of all dives exceeded the aerobic dive limit. The maximum dive depth recorded across all individuals was 903.8m (wd3-CTD3-07) and maximum dive duration was 95.25min (wd3-CTD1-07). These dive and duration values are the maximum recorded for a Weddell seal.

Areas of high use – two-dimensional

Two-dimensional kernel density plots revealed high use areas for each seal and general patterns could be seen amongst foraging types (Fig. 4.5, 4.6 & 4.7). The *mid water column* seals all occupied coastal habitat (Fig. 4.5a – d). At Dumont d'Urville, the high use areas were restricted close to the coast at both Dumont d'Urville and Port Martin (Fig. 4.5a & 4.5b) whilst at the Vestfold Hills; habitat use is confined coastally to the Vestfold Hills region (Fig. 4.5c & 4.5d). Habitat use for individuals in the *benthic* group was further offshore than the pelagic seals (Fig. 4.6a – e) though at Dumont d'Urville, areas of high use are still adjacent to Dumont d'Urville and Port Martin (Fig. 4.6a – d). At the Vestfold Hills (Fig. 4.6e), the high use area was south west of the high use areas of the benthic seals at the Vestfold Hills (Fig. 4.5c & 4.5d). The habitat use by the *upper water column* seals is furthest offshore though no seal moved off the continental shelf (Fig. 4.7a – 4.c). These seals used an area to the east of the Vestfold Hills and travelled as far as Barrier Bay (Fig. 4.7c). These patterns of habitat use are easily identified in the kernel density maps pooled across individuals in each cluster group (Fig. 4.8).

When contrasting the bathymetry of high use areas to low use areas, only *Group 2 – benthic* demonstrated statistically significant relationships. The linear mixed effects models examining the influence of bathymetric features on habitat use (high and low)

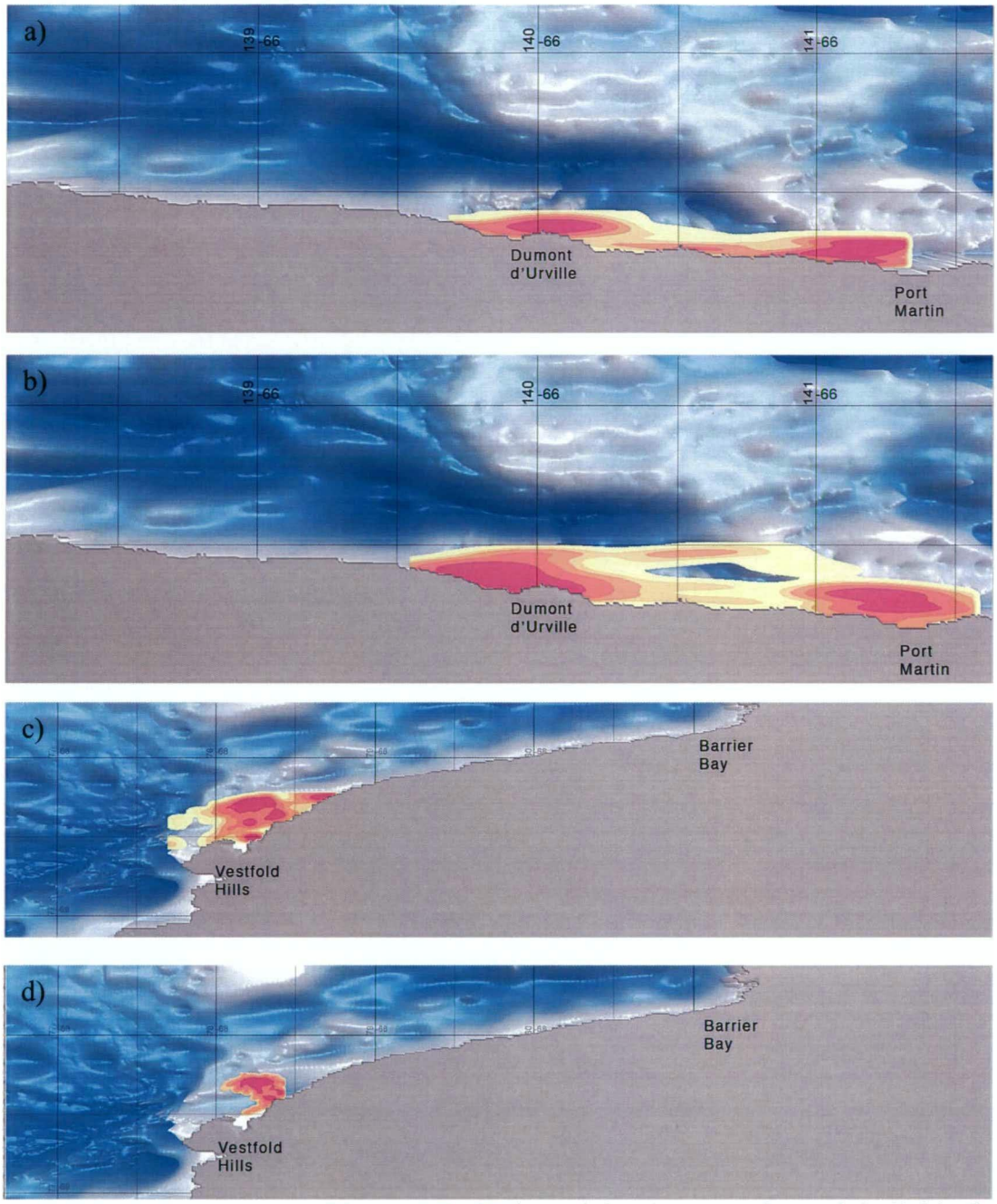


Figure 4.5. 2D kernel density maps for each individual classed in *cluster group 1 – mid water column*; **a)** wd3-CTD1-07, **b)** ct38w-QueenEliz-08, **c)** awru1-A-06, **d)** awru1-B-06. Kernel densities are represented as quantiles of overall density from 0 - 1. Each colour represents a band width of 0.1 – see colour legend (left).

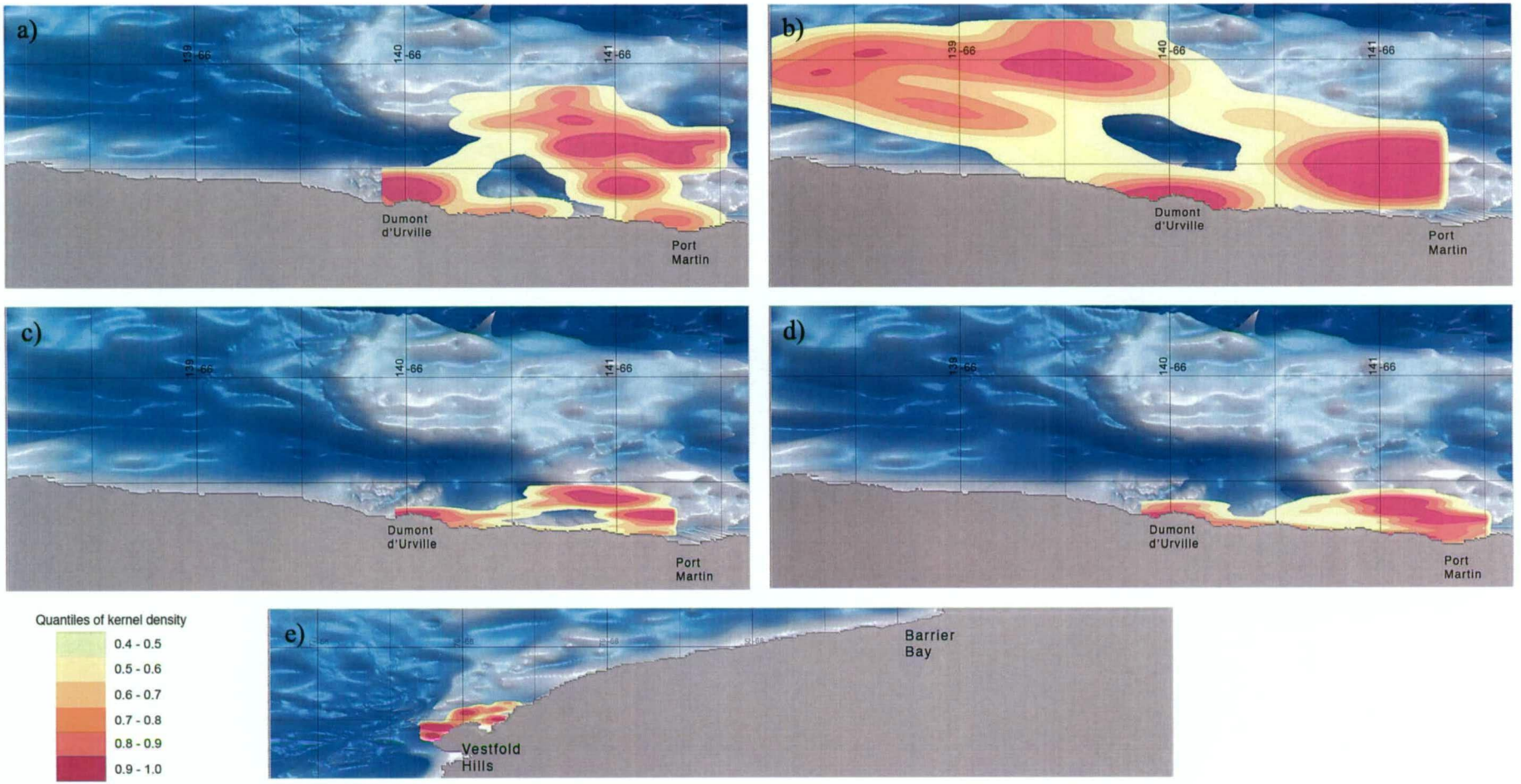


Figure 4.6. 2D kernel density maps for each individual classed in *cluster group 2 - benthic*; **a)** wd3-CTD2-07, **b)** wd3-CTD3-07, **c)** ct38w-Denise-08, **d)** ct38w-Mathilde-08, **e)** awru1-C-06. Kernel densities are represented as quantiles of overall density from 0 - 1. Each colour represents a band width of 0.1 – see colour legend (above).

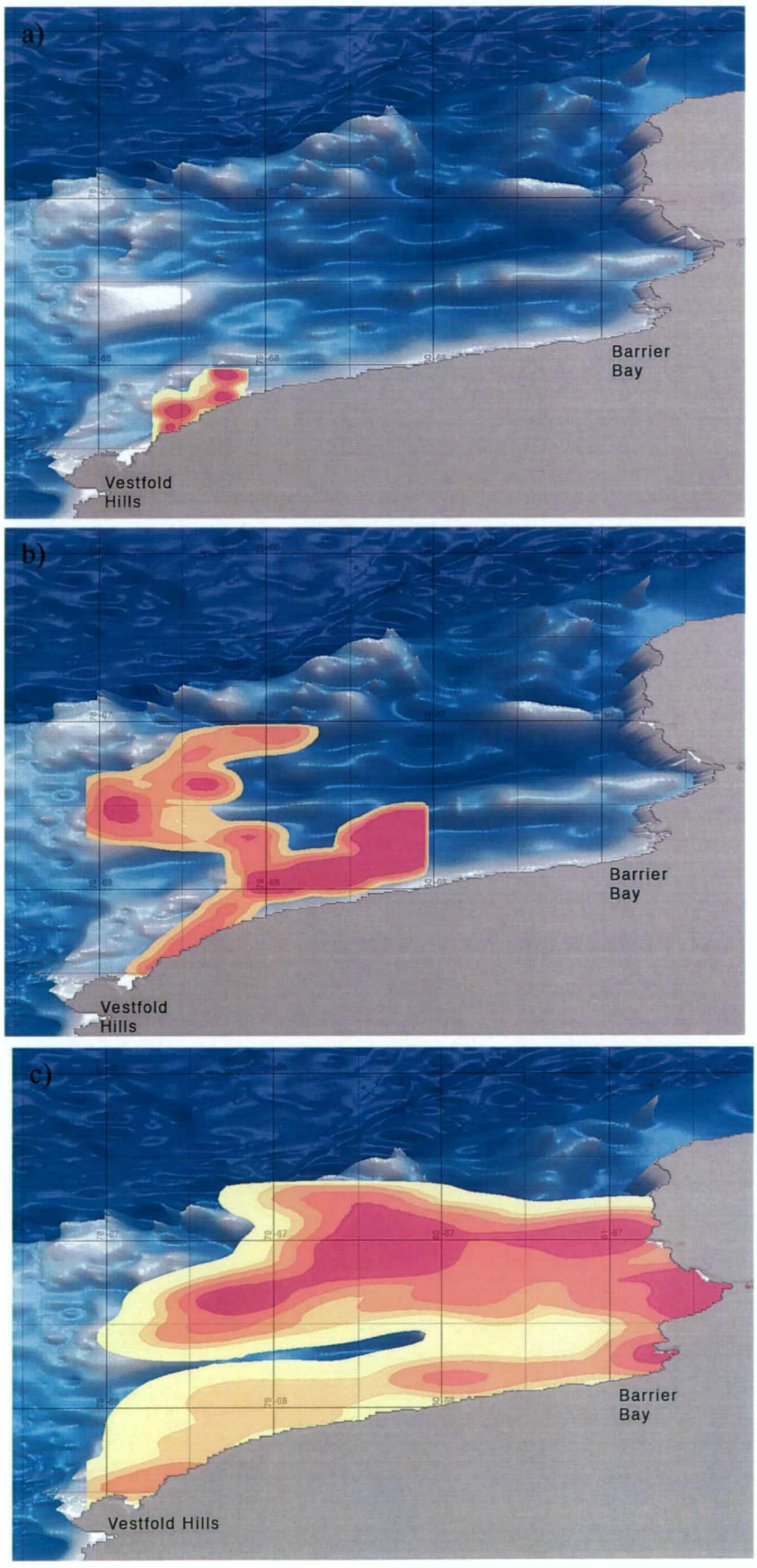
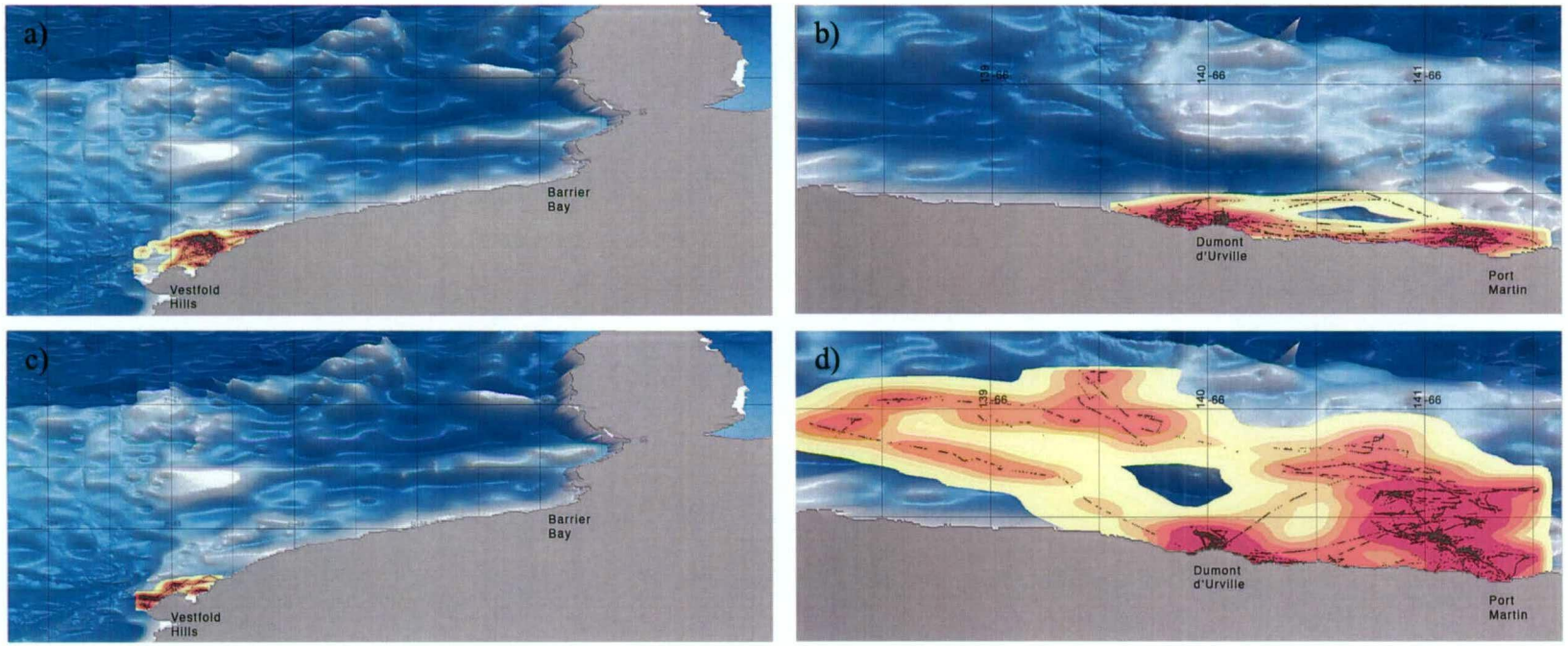
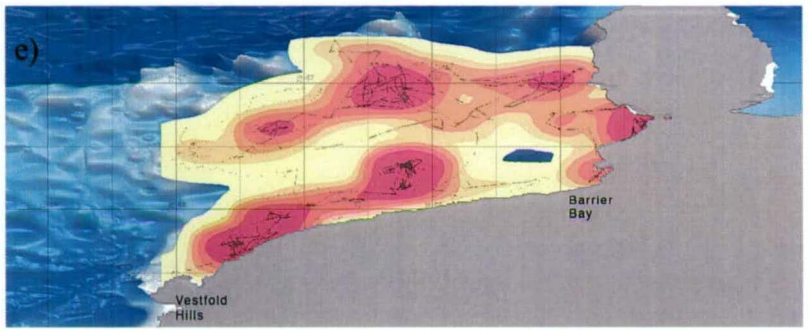


Figure 4.7. 2D kernel density maps for each individual classed in *cluster group 3 – upper water column*; **a)** wd1-10183-06, **b)** wd1-10217-06, **c)** wd1-10213-06. Kernel densities are represented as quantiles of overall density from 0 - 1. Each colour represents a band width of 0.1 – see colour legend (above).





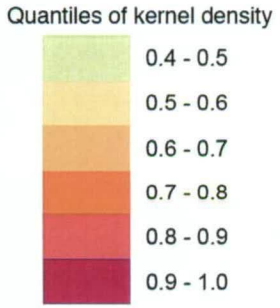


Figure 4.8. 2D kernel density maps for individuals in each cluster group pooled: *Group 1- mid water column* at **a)** Vestfold Hills and **b)** Dumont d'Urville; *Group 2 - benthic* at **a)** Vestfold Hills and **d)** Dumont d'Urville; *Group 3 – upper water column* at **e)** Vestfold Hills. Kernel densities are represented as quantiles of overall density from 0 - 1. Each colour represents a band width of 0.1 – see colour legend (left). Small dark points on each plot represent locations collected.

found *mean bathymetric depth* (AIC = 72.64, log likelihood = -33.32, p = 0.0022), *bathymetric skewness* (AIC = 84.66, log likelihood = -39.33, p = 0.018) and *bathymetric kurtosis* (AIC = 86.06, log likelihood = -40.03, p = 0.034) to be significant. No significant relationship was found between high and low habitat use and *standard error of bathymetric depth* (AIC = 90.43, log likelihood = -42.22, p = 0.49).

For both *Group 1 – mid water column* using a linear mixed effects model and *Group 3 – upper water column* using a generalised linear model, no significant relationship was found between habitat use and *mean bathymetric depth* (*Group 1*: AIC = 22.21, log likelihood = -7.60, p = 0.12; *Group 3*: AIC = 122.79, p = 0.05), *standard error of depth* (*Group 1*: AIC = 23.99, log likelihood = -9.0, p = 0.6 *Group 3*: AIC = 126.38, p = 0.39), *bathymetric skewness* (*Group 1*: AIC = 22.9, log likelihood = -8.45, p = 0.30; *Group 3*: AIC = 125.93, p = 0.27), and *bathymetric kurtosis* (*Group 1*: AIC = 24.23, log likelihood = -9.12, p = 0.9; *Group 3*: AIC = 124.26, p = 0.11).

Specifically, for *Group 2 – benthic*, high use areas were shallower than low use areas (Fig. 4.9a) and were more negatively skewed indicating stronger evidence of seamounts than low use areas, which had a skew approximating 0 (Fig. 4.9b). The kurtosis of high use areas was closer to 0 and more positive than low use areas indicating few extreme values of bathymetric depth tending towards a uniform bathymetry (Fig. 4.9c).

High use areas – three-dimensional

The 3-dimensional kernel densities presented are used purely as a descriptive tool to gain insight into habitat use below the surface. A seal is likely to be most influenced by what is below the surface therefore a 2-dimensional representation of habitat use can be

misleading. This presents problems when trying to relate habitat use to surface environmental variables.

a) b) c)

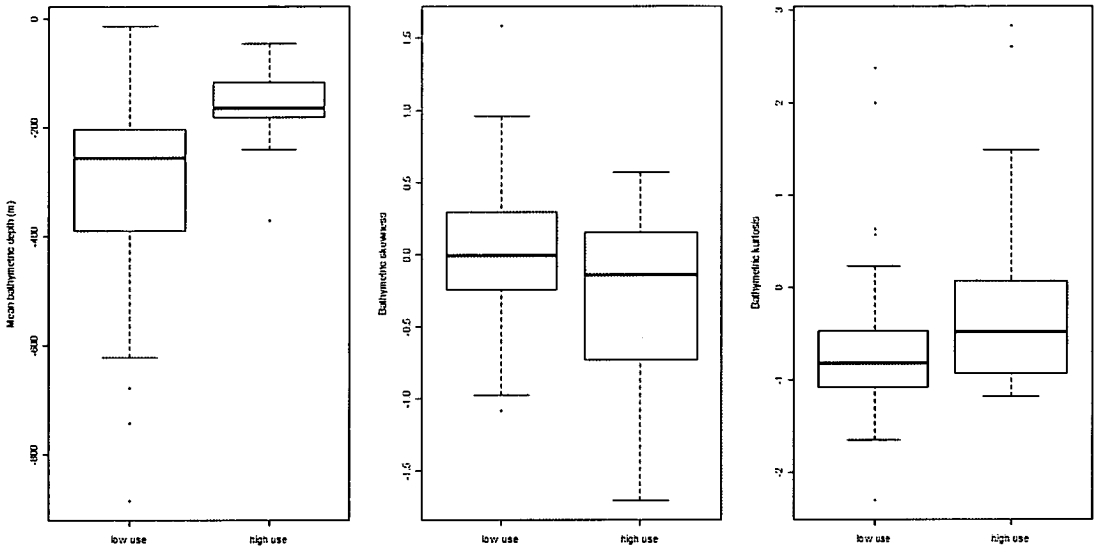


Figure 4.9. Boxplots of high use and low use areas for *Group 2 – benthic*: **a)** bathymetric depth indicating that high use areas occur in shallower depths than low use areas; **b)** bathymetric skewness indicating that high use areas are more negatively skewed than low use areas; and **c)** bathymetric kurtosis indicating that high use areas have a kurtosis closer to 0 than low use areas. Bold horizontal lines in each box represent the median value; the bottom and top of the box show the 25th and 75th percentiles respectively. The vertical dashed lines are representative of 1.5 times the interquartile range of the data showing the spread of data with the points outside this range considered outliers.

3-dimensional kernel density and iso-surface maps indicated the spatial use of each cluster group at depth (Figures 4.10, 4.11 and 4.12). For *Group 1 – mid water column* (Fig. 4.10) and *Group 2 – benthic* (Fig. 4.11), only the densities and iso-surfaces at Dumont d'Urville are shown however both figures are a powerful descriptive tool to summarise each cluster group overall.

In general, *Group 1 – mid water column* dives were not related to bathymetric features and occur primarily along the coastal margin (Fig. 4.10). Areas of high density at the greatest depths were not different to areas of high density at intermediate or

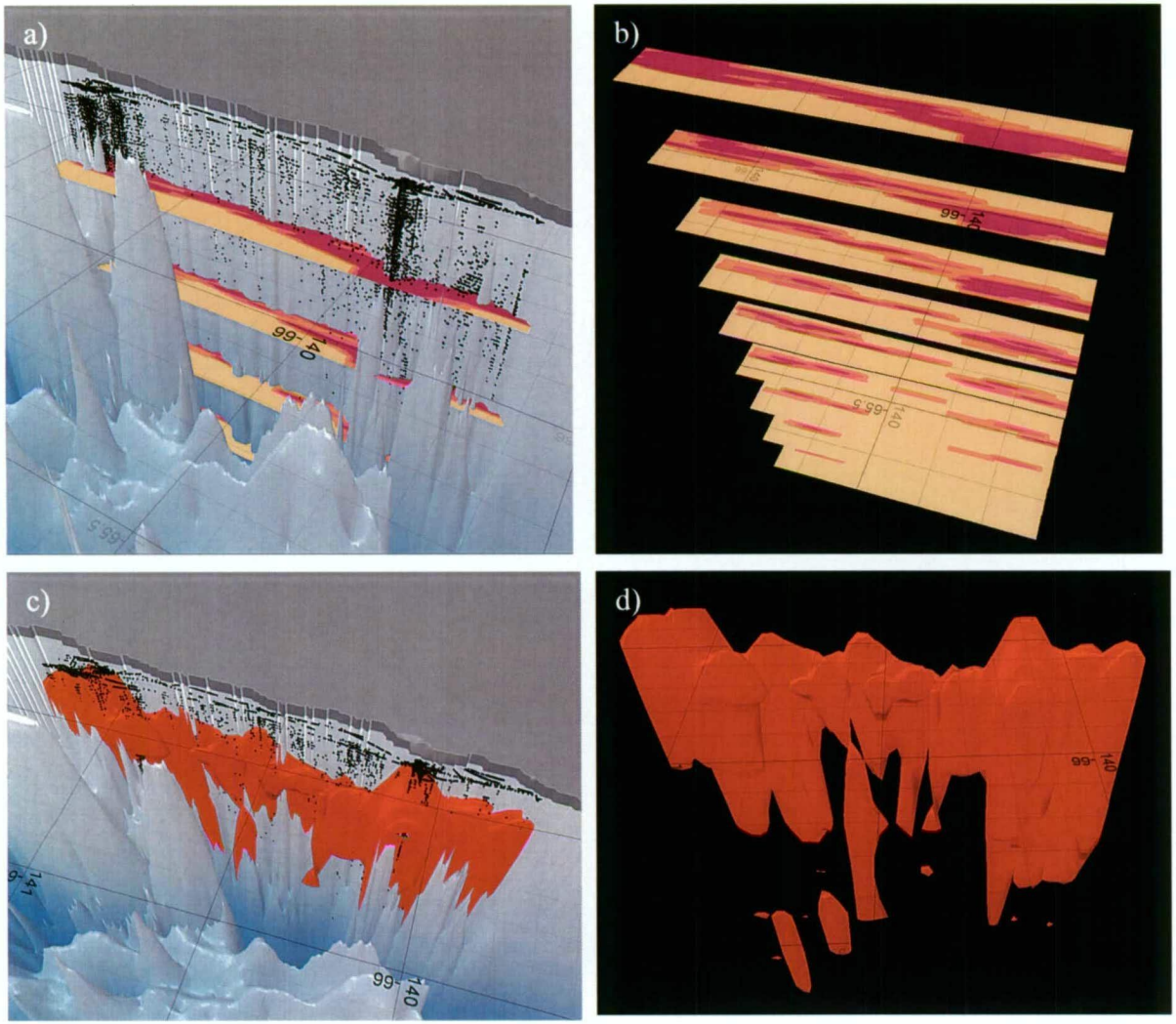


Figure 4.10. 3D kernel density maps of *Group 1 – mid water column* for Dumont d'Urville **a)** with, and **b)** without bathymetry. Each "slice" represents a depth bin. Coloured areas represent kernel density quantiles and the black points represent dive inflection depths. Dives occur against the coastal margin and the highest density of dives occur in the shallow dive bins.
3D 95% isosurface maps **c)** with and **d)** without bathymetry for Dumont d'Urville. These maps detail the distribution of the 95th quantile of all dive inflection depths – essentially, 95% of all dive data fall within this 3 dimensional frame showing the shallow nature of the *Group 1 – mid water column*.

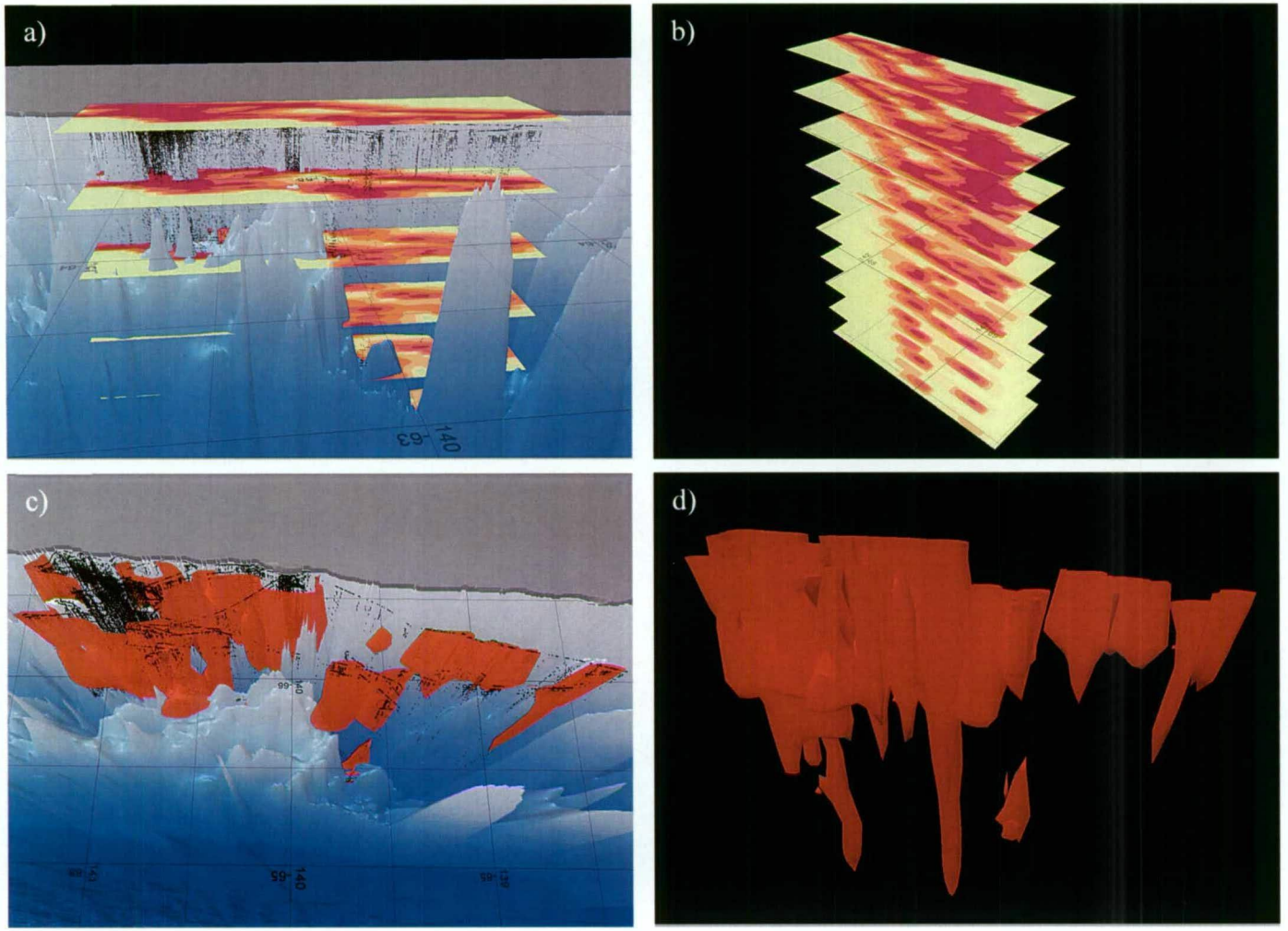


Figure 4.11. 3D kernel density maps of *Group 2 – benthic* for Dumont d'Urville **a)** with, and **b)** without bathymetry. Each "slice" represents a depth bin. Coloured areas represent kernel density quantiles and the black points represent dive inflection depths. 3D 95% isosurface maps **c)** with, and **d)** without bathymetry. These maps detail the distribution of the 95th quantile of all dives – essentially, 95% of all dive data fall within this 3 dimensional frame.

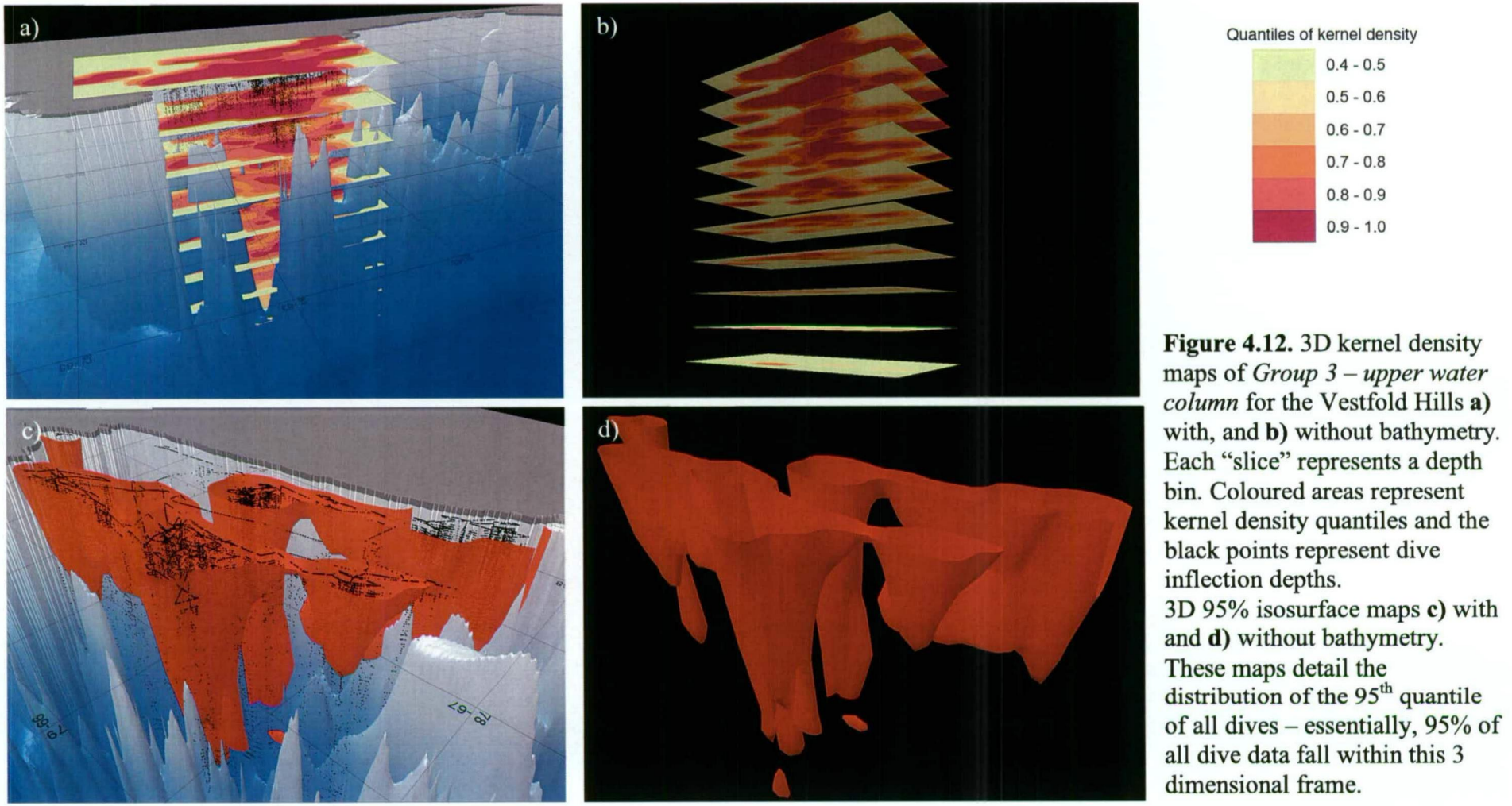


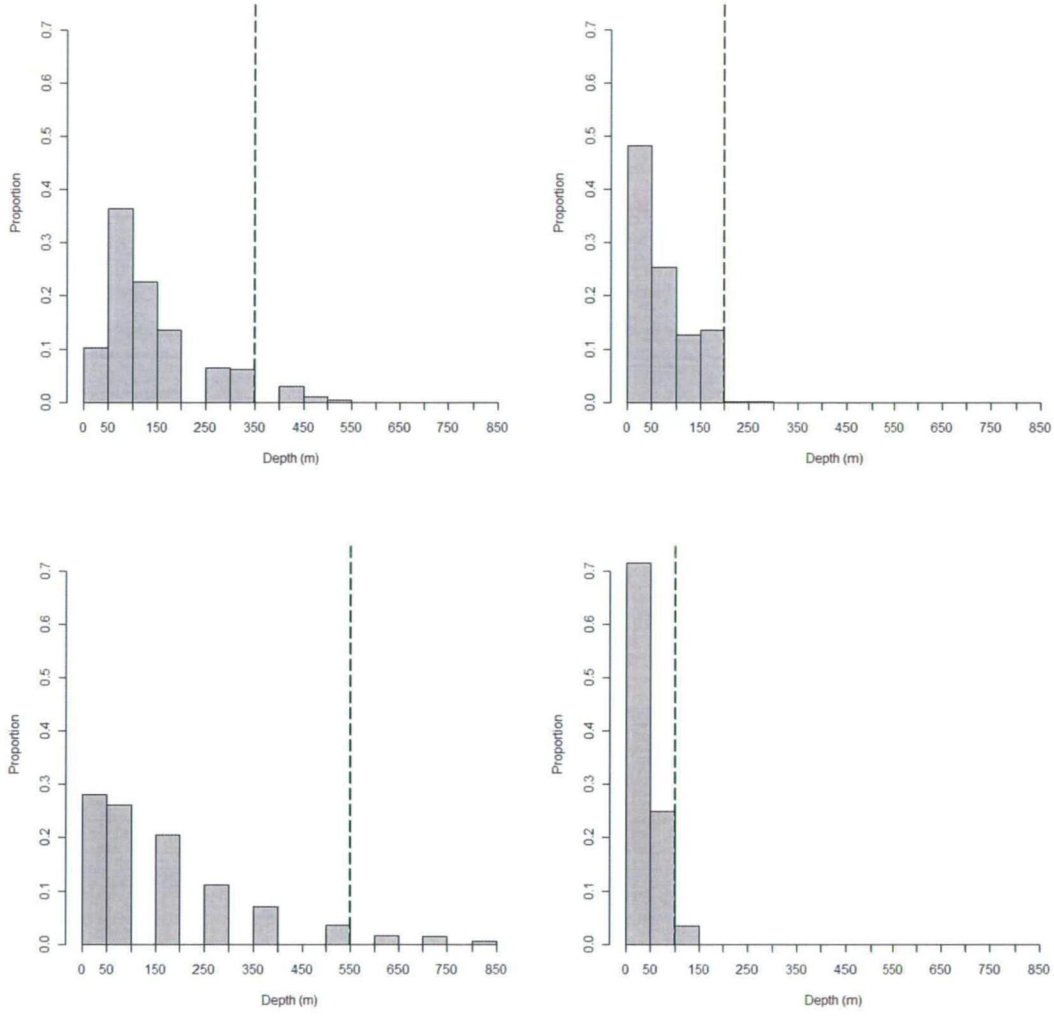
Figure 4.12. 3D kernel density maps of *Group 3 – upper water column* for the Vestfold Hills **a)** with, and **b)** without bathymetry. Each "slice" represents a depth bin. Coloured areas represent kernel density quantiles and the black points represent dive inflection depths.
3D 95% isosurface maps **c)** with and **d)** without bathymetry. These maps detail the distribution of the 95th quantile of all dives – essentially, 95% of all dive data fall within this 3 dimensional frame.

shallow depths. In general, *Group 2 - benthic* dives are closely related to the bathymetry, with seals diving to bathymetric features that are predominantly small mounts that will be referred to as seamounts (Fig. 4.11). For this reason, areas of high use differ with depth for the *benthic* group. In general, for the *Group 3 - upper water column* group, dives were not related to bathymetric features (Fig. 4.12). The distribution of high use areas is similar between depth "slices," with more consistency than the *benthic* group but not as consistently as the *mid water column* group.

There was consistently high use of shallow depths (< 100m; Fig. 4.13) for all foraging groups within high use areas (defined by a kernel density > 0.9). When examining the average quantile density at each depth band or "depth slice" (Fig. 4.14) the pattern of high use of shallow depths was continued with highest average quantile density at the shallowest depth bands. *Group 1 – mid water column* at Dumont d'Urville was the exception to the general pattern of a gradual decline in average quantile density with depth. For *Group 1 – mid water column* at Dumont d'Urville, there is an initial peak in quantile density at the second depth band at 57 – 126m, then the same gradual decline as exhibited by the other groups and sites (Fig. 4.14a). This relationship is also seen in the distribution of high use bathymetric depths with a peak in frequency in the second depth bin, 50 – 100m (Fig. 4.13a)

Behavioural states

State space models revealed that the majority of locations (97.8%) were assigned the class "search." When "transit" did occur, it was often across a substantial distance such as the regular transit periods between Dumont d'Urville and Port Martin or the easterly direction of travel from the Vestfold Hills towards Barrier Bay (Fig. 4.15).



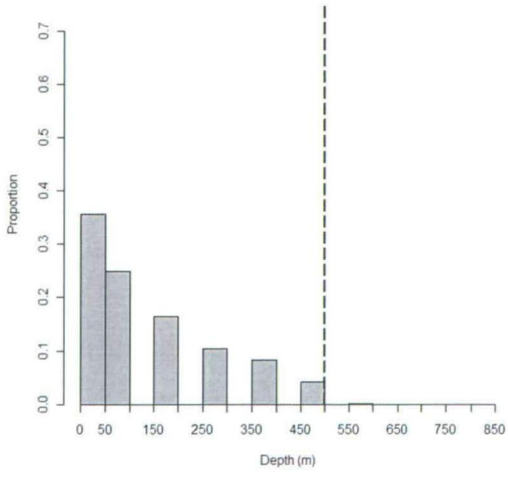


Figure 4.13. Distribution of bathymetric depth for each cluster group within high use areas defined as a kernel density >= 0.9. The x axis shows depths binned at 50m, the y axis shows proportion of data. The vertical dotted line indicates the cumulative proportion of bathymetric depth in the high use area equal to 0.95. **a)** *Group 1 – mid water column* at Dumont d'Urville and **b)** the Vestfold Hills; **c)** *Group 2 – benthic* at Dumont d'Urville and **d)** the Vestfold Hills; **e)** *Group 3 – upper water column* at the Vestfold Hills.

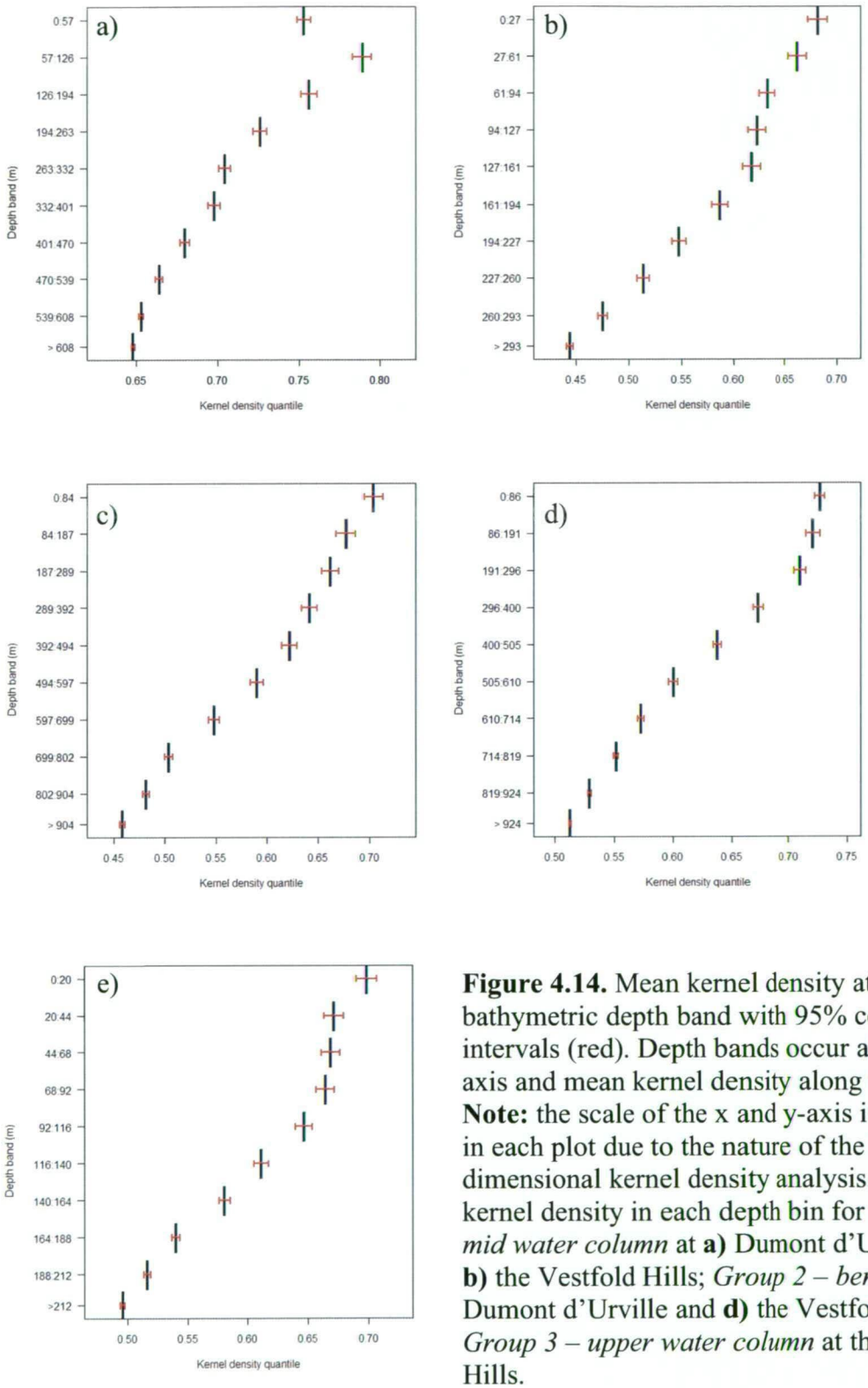


Figure 4.14. Mean kernel density at each bathymetric depth band with 95% confidence intervals (red). Depth bands occur along the y-axis and mean kernel density along the x-axis. **Note:** the scale of the x and y-axis is different in each plot due to the nature of the three-dimensional kernel density analysis. Mean kernel density in each depth bin for *Group 1 – mid water column* at **a)** Dumont d'Urville and **b)** the Vestfold Hills; *Group 2 – benthic* at Dumont d'Urville and **d)** the Vestfold Hills; **e)** *Group 3 – upper water column* at the Vestfold Hills.

For two seals, "transit" mode was not detected at all, and for the remainder no more than 6.8% of locations were classed as transit for any individual (Table 4.6). Seal movement was constrained locally (Table 4.7) with seals moving on average only 4.96 ± 0.13km per day, which may account for the dominance of "search" behaviour. *Group 1 – mid water column* moved on average 4.23 ± 0.16km with a maximum of 34.4km per day, *Group 2 – benthic* moved an average 3.52 ± 0.13km with a maximum of 39.97km per day while *Group 3 – upper water column* moved more than twice as far, 9.25 ± 0.42km with a maximum of 57.30km.

Table 4.6. Seal id and corresponding percentage of locations assigned to the class "search", as opposed to "transit."

Group	Seal	Search
1 – mid water column	awru1-A-06	100.00
1 – mid water column	awru1-B-06	100.00
1 – mid water column	wd3-CTD1-07	96.17
1 – mid water column	ct38w-QueenEliz-08	95.50
2 - benthic	awru1-C-06	98.63
2 - benthic	wd3-CTD2-07	99.04
2 - benthic	wd3-CTD3-07	99.17
2 - benthic	ct38w-Denise-08	99.21
2 - benthic	ct38w-Mathilde-08	98.43
3 – upper water column	wd1-10213-06	93.21
3 – upper water column	wd1-10183-06	99.83
3 – upper water column	wd1-10217-06	97.85

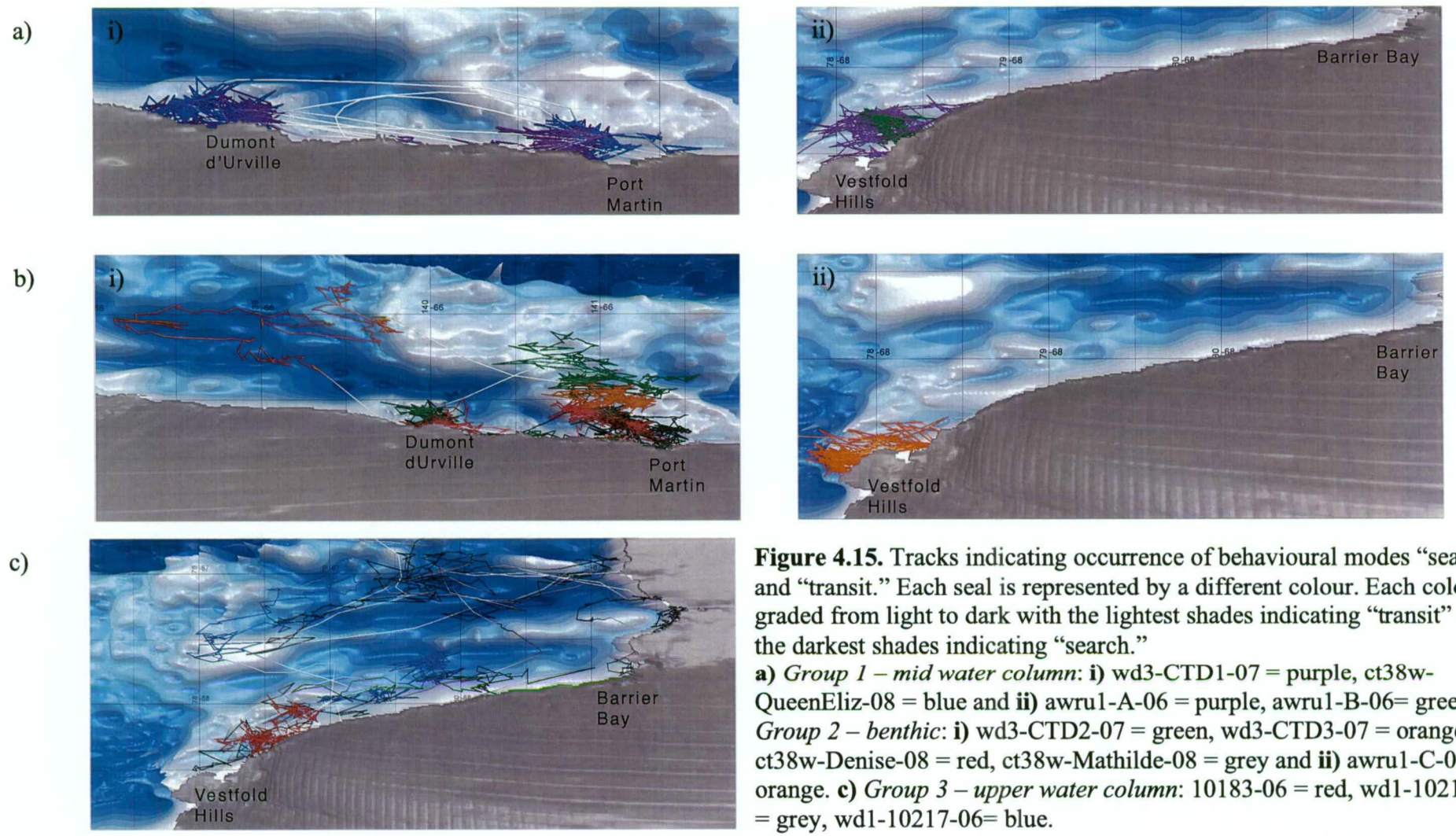


Figure 4.15. Tracks indicating occurrence of behavioural modes "search" and "transit." Each seal is represented by a different colour. Each colour is graded from light to dark with the lightest shades indicating "transit" and the darkest shades indicating "search."
a) *Group 1 – mid water column*: **i)** wd3-CTD1-07 = purple, ct38w-QueenEliz-08 = blue and **ii)** awru1-A-06 = purple, awru1-B-06= green **b)** *Group 2 – benthic*: **i)** wd3-CTD2-07 = green, wd3-CTD3-07 = orange, ct38w-Denise-08 = red, ct38w-Mathilde-08 = grey and **ii)** awru1-C-06= orange. **c)** *Group 3 – upper water column*: 10183-06 = red, wd1-10213-06 = grey, wd1-10217-06= blue.

Table 4.7: Daily and overall movement details for each seal. 'Group' 1= *mid water column*, 'Group' 2 = *benthic* and 'Group' 3 – *upper water column*. Daily and maximum distances indicate that these Weddell seals are predominantly local foragers.

Group	Seal	Mean distance travelled per day (km)	Minimum distance travelled per day (km)	Maximum distance travelled per day (km)	Mean distance from tagging location (km)	Maximum distance from tagging location (km)	Total distance travelled (km)
1	awru1-A-06	6.47 ± 0.48	0.07	31.49	25.46 ± 0.24	50.31	1087
1	awru1-B-06	3.58 ± 0.21	0.007	20.67	29.36 ± 0.14	37.93	835
1	wd3-CTD1-07	3.30 ± 0.22	0.12	22.26	30.92 ± 0.40	58.30	860
1	ct38w-QueenEliz-08	4.35 ± 0.36	0.19	34.40	26.83 ± 0.49	69.17	800
2	awru1-C-06	2.33 ± 0.21	0.02	19.95	7.77 ± 0.08	26.24	655
2	wd3-CTD2-07	6.55 ± 0.44	0.75	39.97	44.14 ± 0.40	75.97	1198
2	wd3-CTD3-07	4.00 ± 0.35	0.07	37.81	46.37 ± 0.54	107.14	848
2	ct38w-Denise-08	2.11 ± 0.15	0.03	14.60	26.83 ± 0.49	69.17	539
2	ct38w-Mathilde-08	3.68 ± 0.29	0.07	34.67	40.21 ± 0.39	64.29	880
3	wd1-10213-06	4.95 ± 0.38	0.09	27.84	42.52 ± 0.30	68.76	707
3	wd1-10183-06	12.84 ± 0.70	0.14	55.0	160.12 ± 0.95	230.74	3030
3	wd1-10217-06	7.80 ± 0.80	0.006	57.30	113.59 ± 0.47	176.35	1240

Influence of environmental variables on diving behaviour

Inter-haulout diving bouts (n = 1025) were as short as 30 seconds containing 1 dive prior to the next haulout or were as long as 9.8 days containing 544 dives before the next recorded haulout. On average, diving bouts contained 40.04 ± 1.30 dives and were 1.14 ± 0.04 days long.

Cox proportional hazards models attempt to relate surface environmental variables to temporal habitat use by modelling inter-haulout diving bout duration against environmental variables. Two-dimensional representations of habitat use can be misleading, as they don't account for the features below the surface that influence the seal. Diving bout duration is, to a certain extent, independent of bathymetric features, varies greatly in duration and reflects directly on the time available to successfully forage making it a useful parameter for investigation of foraging behaviour. We included *seal* nested within *site* as a random variable in these models. We did not include the cluster groups as a random variable as seals in 2 of the 3 groups occurred at both sites. Each site experiences contrasting weather conditions due to local landmasses. For example, there was a distinct lack of dominant southerly and strong winds at the Vestfold Hills compared to Dumont d'Urville and much higher ice concentrations at Dumont d'Urville than the Vestfold Hills. Therefore examining the influence of weather on groups with members from both the Vestfold Hills and Dumont d'Urville was not appropriate.

The best of the 158 mixed effects CPH models included *ice*, *month*, *wind speed* and *temperature*. Of the top ten models ranked by AIC_c, *month* occurred in all 10 models while *ice* occurred in 9 of the 10 models (Table 4.8). The best model according to the AIC and with an akaike weight of less than 2, was:

$$h(t) = \exp(\beta_i ice_i - \beta_j month_j - \beta_k windsp_k + 0.017 temperature + b) h_0(t),$$

where *ice* is ice concentration in the *i* category, *month* is the time of year in the *j* category, *wind speed* is wind speed in the *k* category, *temperature* is air temperature (°C) and *b* is the per individual random effect nested within site. Estimated coefficients, hazards ratios, standard errors and confidence intervals for this model are presented in Table 4.9.

When examining the estimated coefficients of the top model (Table 4.9), the "risk", or likelihood of a diving bout ending in ice > 98.5% concentration is 1.7 times higher than for the baseline concentration (< 58.5%). For all months there is a decreased risk of the diving bout ending relative to March. For all wind speed categories there is decreased risk of the diving bout ending (ranging from 32%, 35% and 37% less risk respectively) in relation to the baseline wind speed of < $8ms^{-1}$. As temperature increases, the risk of the diving bout ending also increases 17% per 2°C.

The standard deviation of the variance component attributed to each site and individual ($\sqrt{0.0007}$ and $\sqrt{0.044}$ respectively) indicates that the average spread of the risk of the diving bout ending between sites is 29% ($e^{0.029} \approx 1.029$) higher or lower than the overall risk, while the per-individual variability in the risk of ending the diving bout is on average ($e^{0.210} \approx 1.233$) 1.2 times higher or lower than the overall risk. In other words, a diving bout is more likely to end in very high ice concentrations, is less likely to end as wind speed increases, is less likely to end as the season progresses and is more likely to end as air temperature increases. However, this overall relationship can vary at each site (by 29%) and between individuals (by 1.2 times). The variability attributed to individual was greater than that attributed to site.

Table 4.8: Top ten models as ranked by their AIC with most parsimonious at the top for diving bout duration in relation to the ice concentration, month, bearing, bathymetric depth, wind direction, wind speed and temperature. Akaike's information criterion corrected to actual sample size (AIC_c) is presented along with AIC_c differences (Δ_i), Akaike weights (w_i), evidence ratios, coefficients of determination (R^2), penalised log likelihoods (log(L)) and penalised degrees of freedom (df). Sample size is 1025. Ice is sea ice concentration in 4 categories (< 57.5%, > 57.5-89.5%, > 89.5-98.5%, >98.5%), Month is time of year in 5 categories (March, April, May, June, July, August), Wind sp is wind speed in 4 categories (< 8ms, > 8 – 12ms, > 12-22ms, > 22ms), Temperature is air temperature in °C, Wind dir is dominant wind direction in 4 categories (north, south, east, west) and Bearing is dominant seal bearing in 4 categories (north, south, east, west).

Model	AIC_c	Δ_i	w_i	evidence ratio	R^2	log(L)	df
Ice + Month + Wind sp + Temperature	12039.9	0.0	0.67	1.00	0.154	-6058	14.86
Ice + Month + Wind dir + Wind sp	12042.7	2.8	0.16	4.08	0.158	-6059	17.08
Ice + Month + Bearing + Wind sp	12044.7	4.8	0.06	10.93	0.156	-6048	17.07
Ice + Month + Bearing + Wind dir	12046.5	6.7	0.02	27.81	0.152	-6029	19.39
Ice + Month + Wind sp	12046.7	6.8	0.02	29.40	0.148	-6055	17.17
Ice + Month + Depth + Wind sp	12047.6	7.7	0.01	47.54	0.148	-6055	16.73
Ice + Month + Wind dir	12048.1	8.2	0.01	60.39	0.143	-6061	14.99
Ice + Month + Wind dir + Temperature	12048.3	8.5	0.01	68.40	0.144	-6053	17.96
Ice + Month + Wind dir + Depth	12048.9	9.0	0.01	89.37	0.143	-6013	22.64
Month + Wind dir + Wind sp + Temperature	12050.3	10.4	0.00	181.16	0.141	-6028	20.39

Table 4.9: Estimated coefficients (β), hazards ratios (e^{β}), standard error of estimated coefficients, 95% confidence intervals for hazards ratios and sample sizes (n) of the mixed effects Cox proportional hazards model for the covariates affecting the risk of a diving bout ending. Risk classed as '+' or '-' indicates an increase or decrease in risk of the diving bout ending. An $e^{\beta} < 1$ indicates decreased risk of a diving bout ending whilst an $e^{\beta} > 1$ indicates increased risk of a diving bout ending.

Variable	n	β	e^{β}	se(β)	CI(eβ)	risk
Ice (< 57.5%)	232	-	-	-	-	
Ice (57.5%-89.5%)	401	-0.126	0.882	0.088	0.74 to 1.05	-
Ice (89.5%-98.5%)	275	0.085	1.089	0.101	0.89 to 1.33	+
Ice (>98.5%)	117	0.536	1.709	0.129	1.33 to 2.20	+
Month (Mar)	172	-	-	-	-	
Month (Apr)	224	-0.373	0.689	0.107	0.56 to 0.85	-
Month (May)	272	-0.297	0.743	0.108	0.60 to 0.92	-
Month (Jun)	146	-0.646	0.524	0.127	0.41 to 0.67	-
Month (Jul)	109	-0.864	0.421	0.135	0.32 to 0.55	-
Month (Aug)	102	-0.802	0.449	0.137	0.34 to 0.59	-
Wind speed (< 8ms)	251	-	-	-	-	
Wind speed (8ms - 12ms)	249	-0.383	0.682	0.094	0.57 to 0.82	-
Wind speed (12ms - 22ms)	305	-0.424	0.655	0.092	0.55 to 0.78	-
Wind speed (> 22ms)	220	-0.461	0.631	0.106	0.51 to 0.78	-
Temperature	1025	0.017	1.017	0.007	1.00 to 1.03	+

DISCUSSION

Weddell seal foraging strategies

The foraging strategies of marine predators exist on a continuum between strictly benthic to strictly pelagic behaviours (Villegas-Amtmann *et al.* 2008). A species that demonstrates a combination of foraging strategies often does so in response to the habitat available (Goebel *et al.* 1991; Hindell *et al.* 1991; Bailleul *et al.* 2007), likely due to its influence on prey behaviour and availability (Bailleul *et al.* 2007). In a constant environment, variation in foraging strategy between individuals may evolve as a response to weak inter-specific competition with strong intra-specific competition for

limited resources (Estes *et al.* 2003). Temporal variation in prey availability may then mediate temporal variation in foraging strategies.

Studies into the diet of Weddell seals suggest that this species has the capacity to switch foraging techniques according to prey availability, such as the switch from pelagic foraging on *Pleuragramma antarcticum* one year to almost entirely benthic fish the next (Plotz *et al.* 1991). Weddell seals in McMurdo Sound throughout the winter also forage on *P. antarcticum* and other mid-water species such as squid however, occasionally, they shift to benthic prey (Testa 1994).

The Weddell seals in this study used both pelagic and benthic strategies, but with no temporal pattern to their individual foraging strategies, reflecting the opportunistic nature of their feeding (Hindell *et al.* 2002). From these pelagic and benthic behaviours, published information on diet (Lake *et al.* 2003) and scat analyses of the Dumont d'Urville population (V. Andrews-Goff unpublished data), we can infer the likely prey of the seals in this study. Important benthic prey would include adults of *Trematomus* spp, *Channichthyidae* spp and *Pleuragramma antarcticum* on its downward diel migration (Robison 2003). Amongst the potential pelagic prey are the pelagic fishes, *Pleuragramma antarcticum* and *Dissostichus mawsoni* along with cephalopods, predominantly *Psychroteuthis glacialis*. Crustaceans are also a potential diet item, most probably *Chorismus* spp. Even with each seal employing a mix of foraging strategies presumably reflecting benthic and pelagic prey choice, it was possible to assign a dominant foraging strategy with five seals classified as predominantly benthic foragers and seven seals classified as pelagic foragers.

The pelagic foraging seals could be further divided into mid water column and upper water column specialists. The seals in the upper water column group foraged over deeper depths (an average of 460m) and consequently dove deeper (105m) than the mid

water column group who occurred over a much shallower bathymetric depth (157m) and also performed shallower dives (70.8m). The upper water column divers spent more time diving overall but their average dive duration was less than that of the mid-water column divers, which were also more likely to exceed their ADL. Finally, the upper water column divers tended to be a more mobile group than the mid water column divers and, perhaps most importantly, occurred only at the Vestfold Hills. The mid water column group was spread evenly between Dumont d'Urville and the Vestfold Hills. Even within one location (the Vestfold Hills) and one foraging group (pelagic), individual variation can be so distinct as to create two subgroups of foraging behaviour within the pelagic classification.

Although individuals from Dumont d'Urville dominated the benthic foraging group, it also contained one individual from the Vestfold Hills. Animals that employ benthic foraging strategies have the potential to operate at their maximal physiological capacity (Costa and Sinervo 2004), commonly approaching or exceeding their aerobic dive limit (Costa and Gales 2003). Pelagic foragers on the other hand have the capacity to operate within their physiological capacity by targeting prey that occurs mid-water. Pelagic foragers have the capacity to locate their prey earlier in the dive, and if the need arises, draw on a greater physiological reserve to pursue prey to depth or at depth and forage longer (Costa and Sinervo 2004). However, for the Weddell seals in this study, benthic divers were the least likely to exceed their ADL and did not dive as deeply as the other seals. In this case, it is the pelagic foragers that are more likely to be operating at maximal physiological capacity. This could be a reflection on the more predictable and robust nature of a benthic food compared to pelagic prey (Costa and Sinervo 2004) which are more influenced by the biological features of the ocean (Bailleul *et al.* 2007). However, in the absence of data detailing the foraging success of the individuals in this

study, we have to assume that all individuals were successful foragers; getting the energy required regardless of the foraging strategy employed.

Bathymetry was only important for benthic foragers, with areas of relatively high use characterised by shallower depths and small seamounts. The seamounts add a level of complexity to the benthic habitat. Structurally complex habitats provide a larger array of competitive and predatory refuges and sustain more diverse communities (Diehl 1992). In addition, seamounts are thought to trap downwardly diurnally migrating plankton and are thereby able to support large pelagic and bentho-pelagic fish communities (Rogers and Bryden 1997). For the pelagic foragers, bathymetry may not play a role in determining the areas of high use as the presence of pelagic prey may be more influenced by aspects such as sea ice mediated productivity (Bailleul *et al.* 2007).

For all three foraging strategies, highest kernel densities occurred in shallow waters used to traverse through whilst travelling to and from foraging depths. Therefore, shallow depths are an important habitat for Weddell seals in terms of the high occupancy of these areas, but the extent to which this reflects foraging importance is uncertain. Weddell seals hunt fish in the sub-ice zone, blowing air into crevices to flush out *Pagothenia borchgrevinki* and catching small prey in soft platelet ice (Davis *et al.* 1999). Surface waters therefore can be regarded as an important habitat to Weddell seals in terms of occupancy and potentially as foraging habitat.

The Weddell seals in this study remained within 50km of their tagging location on average. The state space model indicated that these seals were almost continuously in a state of "search", however this was probably a reflection on the very small distances moved daily (5km on average) and may highlight the fact that these state space models are not appropriate for local foragers. This local habitat use is quite different to the winter behaviour of other seals associated with the Antarctic ice – the

majority of crabeater seals *Lobodon carcinophagus* stayed within 300km of their tagging location (Burns *et al.* 2004) and leopard seals tend to disperse northwards during the winter, most likely in relation to the winter ice edge (Jessopp *et al.* 2004). The winter movements of Ross seals *Ommatophoca rossii* are similar to those of the leopards seals in that they migrate north in winter and most likely access the area between the northern limit of the pack ice and the Antarctic convergence (Jessopp *et al.* 2004). The key difference between Weddell seals and the other ice seals is their unique ability to maintain breathing holes in the ice by abrading the sea ice with their teeth (Bertram 1940; Stirling 1969a) which allows occupation of the fast ice environment year round. Whilst occupation of the winter fast ice environment would reduce inter-specific competition, it results in exposure to harsh environmental conditions associated with the continental Antarctic winter.

Individual variability

Individual specialisation in foraging strategies is more common in environments with fewer competing species (Bolnick *et al.* 2003) such as the Antarctic winter ice environment. The Weddell seal is one of four ice-obligate seals (crabeater, leopard, Ross and Weddell) and two ice-tolerant seals (southern elephant *Mirounga leonina* and Antarctic fur seal *Arctocephalus gazella*) (Siniff *et al.* 2008) within the Southern Ocean ecosystem. Each of these species has its own habitat specialisation and unique behaviours that result in little overlap in habitat use or diet (Siniff 1991). Presuming that inter-specific competition is low, then strong intra-specific competition is needed to drive diversification into multiple foraging strategies (Estes *et al.* 2003). This is a strong possibility for Weddell seals that remain close to their tagging locations and

presumably concentrate around a limited number of breathing holes and cracks to access air in between dives (Hindell *et al.* 2002).

The ability of Weddell seals to utilise contrasting foraging strategies indicates a level of phenotypic plasticity within the populations at Dumont d'Urville and the Vestfold Hills. Phenotypic plasticity allows a shift in response to differing environmental conditions (Bradshaw 1965) through modifications of phenotypic characteristics (anatomical, morphological, behavioural or physiological) (Terraube *et al.* 2010). The Weddell seals at Dumont d'Urville and the Vestfold Hills shift their foraging behaviour along a spectrum that exists between generalist and specialist foraging relative to environmental aspects such as prey availability. Even though each seal could be classed as a predominantly benthic or pelagic forager, all seals utilised both strategies.

When all prey items yield an equal benefit, an equilibrium frequency of different foraging types should occur (Partridge and Green 1985). The value of a prey item depends on its energetic and nutritive content plus its availability (Estes *et al.* 2003). Availability is mediated by the foraging preference of the predator. If all individuals were to specialise on the most valuable prey item, prey depletion would lead to a decrease in the value of that prey item, leading some individuals to specialise in other prey. This results in a population regarded as generalist, but made up of individual specialists (*i.e.* marine herbivores (Poore and Hill 2006), seabirds (Woo *et al.* 2008) and reviewed by Bolnick *et al.* (2003)). The overall foraging strategy of Weddell seals in this study can also be regarded as generalist, encompassing both the pelagic and benthic marine habitat with individuals specialising to a degree in benthic and epipelagic foraging strategies within a single year. Within this individual specialisation

there may be to some extent opportunistic foraging mediated by prey availability (Roper 1994; Elmhagen *et al.* 2000).

The foraging strategy of Weddell seals in this study varied between individuals within and between sites. This has important implications for conservation and predictions of the potential impact of climate change on this species, as individuals within the one population will respond differently to changes in their environment. Generalist populations however, are robust to change as they can occupy a range of habitats and have a larger range of prey available for consumption than specialists (Laidre *et al.* 2008). Generalist populations therefore are at less risk of extinction in the face of catastrophic environmental shifts (McKinney 1997; Munday 2004).

The influence of environmental variables on diving bouts

Weddell seals are a perfect test case to examine the influence of environmental variables on behaviour. Sea ice conditions constrain these individuals to the Antarctic continental shelf for the majority of the year, with very little opportunity to escape any adverse effects imposed by factors such as violent storms. As opposed to loose ice or open ocean, dense ice environments are simplified with vertical gradients in environmental parameters such as sea surface temperature, sea surface height and chlorophyll-a not important.

Long term data sets for the Weddell seals of McMurdo Sound have described the impact of a broad scale climatological pattern, El Niño – Southern Oscillation on population dynamics (Testa *et al.* 1991; Proffitt *et al.* 2007) via its influence on sea ice concentration and extent and consequently the influence on prey availability. The same relationship has been postulated for Weddell seals of the Vestfold Hills (Lake *et al.* 2008). For the McMurdo population, a range of relationships with sea ice have been described with increased sea ice in the post weaning period leading to decreased

foraging success for pregnant females (Hadley *et al.* 2007a), summers of extensive sea ice concentration leading to reduced foraging success of pregnant Weddell seals (Proffitt *et al.* 2007), years of extensive winter sea ice followed by years of higher survival for adult females (Hadley *et al.* 2006), females that were more likely to give birth to their first pup in the spring following a winter characterised by heavy sea ice (Hadley *et al.* 2007b) and finally, increasing thickness of near shore ice resulting in fewer pups being born possibly due to the loss of predictable cracks in the ice used to access preferred pupping sites (Siniff *et al.* 2008). For the Weddell seals of Arthur Harbour, on the Antarctic Peninsula, numbers are declining presumably due to the decrease of fast ice in the region necessary for breeding (Siniff *et al.* 2008). Low reproductive rates experienced by Weddell seals at the Vestfold Hills throughout the 1990s, which were not apparent for the McMurdo Sound population, are likely to be attributable to conditions of the local environment as opposed to a broad scale climatological pattern such as El Niño – Southern Oscillation (Lake *et al.* 2008).

Some short-term data sets have been able to establish links between Weddell seal behaviour and the local environment. In particular the link between favourable weather conditions such as high temperature and low wind speed with a higher incidence of haulout has been noted for at least three different populations (Lake *et al.* 1997; Sato *et al.* 2003b; Andrews-Goff *et al.* 2010).

Our 3-year data set was able to establish a link between diving behaviour and the local environmental variables ice concentration, wind speed and temperature using mixed effects Cox proportional hazards models, with the top model able to explain 15.4% of the variability within the data set. In the context of studies that attempt to link animal behaviour to environmental variables, the ability of the mixed effects Cox proportional hazards model to explain that degree of variance is promising. The Cox

proportional hazards model is regarded as a semi-parametric model with no particular form of probability distribution assumed for the "survival times" (in this case, diving bout duration) (Collett 2003). As such, it is a flexible approach that does not involve assigning an arbitrary or potentially incorrect distribution to the response variable (Fox 2002) which may enhance their ability to perform well on complex biological data.

The mixed effects Cox proportional hazards models enable a series of statements to be made regarding the influence of the environment on diving bouts: i) diving bouts were more likely to end in very high ice concentrations (> 98.5%) as opposed to light ice concentrations, ii) diving bouts were less likely to end in wind speeds exceeding $8ms^{-1}$ and iii) diving bouts were more likely to end as temperature increased. Weddell seals therefore choose to terminate a diving bout when the weather conditions were favourable in accord with the tendency for these same Weddell seals to haulout in more favourable weather conditions (Andrews-Goff *et al.* 2010). This could indicate that the thermoregulatory requirements throughout winter may influence the diving behaviour of the seals, as they are more likely to continue diving when faced with cold and windy conditions. The fact that haulout behaviour and diving bout behaviour are both influenced in the same way indicates that food availability is not the primary driving factor behind these behaviours. Therefore, for the three years of this study, it is probable that prey was not a limiting resource.

The decision to terminate a diving bout in heavy ice (> 98.5% concentration) is likely linked to the fact that Weddell seals must be able to access a reliable breathing hole or ice crack after diving bouts under ice (Wartzok and Davis 1992). Throughout the winter, Weddell seals occupy the fast ice environment, which by nature, is regarded as a very heavy ice environment. However within this ice environment is the possibility to access patches of lighter ice and areas of open water (see chapter 3) and pressure

cracks (Lake *et al.* 2005b). The need to maintain a breathing hole may not be relevant to the Weddell seals at Dumont d'Urville and the Vestfold Hills. Anecdotal evidence suggests that breathing holes are absent in the fast ice environment around Dumont d'Urville throughout the winter and this area also experiences frequent fast ice clear out events (Massom *et al.* 2009). Breathing holes may not be essential for accessing open water at the Vestfold Hills as Weddell seals within the fast ice haulout along ice cracks (Lake *et al.* 2005b). For these eastern Antarctic populations therefore, maintenance of a breathing hole may not be as important to the occupancy of the winter sea ice environment as other populations such as McMurdo Sound (Stirling 1969b). If the Weddell seals of Dumont d'Urville and the Vestfold Hills are using cracks as their primary access to winter haulout sites and for breathing, and thinner ice is more likely to crack than thicker ice (Lake *et al.* 2005b), then the higher tendency for diving bouts to be terminated in very heavy ice conditions is likely to be a reflection of the lack of ice cracks in very heavy ice environments.

Month was also included in the top model and indicated that the risk of a diving bout ending was less for all months relative to March. This also agrees with the haulout data for the same individuals that found that haulout duration decreased as the season progressed from March into the austral winter and autumn (Andrews-Goff *et al.* 2010). In March, Weddell seals remain hauled out for extended periods to moult after which there is no biological need to remain hauled out for extended periods until the breeding season the following spring (Andrews-Goff *et al.* 2010). Consequently, the risk of a diving bout ending is decreased between April and September in relation to March.

With the Weddell seals in this study employing differing but flexible foraging strategies, switching between benthic and pelagic foraging may compensate for any environmental change that influences prey availability. However, this individual

variability makes predictions of the actual response of these seals to environmental change difficult to ascertain with the potential for multiple, diverging responses within a single population. Weddell seals not only react to large-scale climatic anomalies but also to the local scale environment with diving bout behaviour modified by temperature, wind and high ice concentrations. Weddell seals are therefore vulnerable to change that occurs both locally, regionally and throughout their circumpolar range. As such, climate change has the potential to influence Weddell seals through long term changes at a broad scale *i.e.* changes in sea ice extent, and short term changes at a local scale *i.e.* increased winds and decreased temperature associated with a local event such as a storm.

5. General Discussion

In the past, Earth has experienced both intrinsic (e.g. volcanic activity) and extrinsic (e.g. large meteorite strikes) events resulting in population declines, species extinctions and ecosystem collapse (Hoegh-Guldberg and Bruno 2010). An overwhelming amount of evidence suggests that the scale of change resulting from these historic events is comparable to the rapid anthropogenic climate change currently occurring (IPCC 2007). With many of these changes already manifesting rapidly in the world's oceans, often in a non-linear fashion (Hoegh-Guldberg and Bruno 2010), the adaptive capacity of many marine species is being tested.

Marine mammals have evolved to accommodate fluctuations in their physical and biological environment through diverse life history patterns (Costa and Crocker 1996). For Antarctic marine mammals, these life history patterns are woven tightly into the dynamics of the sea ice environment; its seasonality, extent and structure (Massom and Stammerjohn 2010). In recent years, the effects of climate change have manifested in the Antarctic ecosystem via changes in Antarctic sea ice extent, timing and thickness (Massom and Stammerjohn 2010). The consequences have involved a broad range of Antarctic predators including Adélie penguins (McClintock *et al.* 2008), Emperor penguins (Barbraud and Weimerskirch 2001) and Weddell seals (Siniff *et al.* 2008) by influencing their survival, foraging success, access to breeding sites and reproductive success.

Sea ice decline in the Arctic has been more evenly distributed than in the Antarctic due to the differing geology of the poles. The Arctic has ocean at the pole contrasting with Antarctica that has land at the pole (Parmesan 2006). Consequently, Arctic marine mammals are losing sea ice habitat throughout their entire range. Like

Antarctic marine mammals, the life history and foraging ecology of Arctic marine mammals is finely tuned to the Arctic sea- ice environment leaving them vulnerable to any sudden and large scale unidirectional change (Laidre *et al.* 2008). March Arctic sea ice has declined from 16.5 million km^2 in 1979 to 15.25 million km^2 in 2009 and summer sea ice is projected to disappear completely by 2037 (Hoegh-Guldberg and Bruno 2010). As a consequence, much research is focussed on anticipating the likely response of Arctic marine mammals to global climate change and sea ice loss and applying conservation measures (Bluhm and Gradinger 2008; Moore and Huntington 2008; Ragen *et al.* 2008).

A range of factors may contribute to the sensitivity of polar marine mammal species to climate change. Laidre *et al.* (2008) proposed criteria to assess the sensitivity of Arctic marine mammals to climate change including aspects of population size and range, habitat and diet specificity and life history. Similarly, Siniff *et al.* (2008) described the likely effects of environmental change on Antarctic seals by incorporating responses to recent climate change with current and projected change and producing a likely future scenario. For Weddell seals, Siniff *et al.* (2008) used long term data sets from McMurdo Sound and the Antarctic Peninsula to assess the potential effect of climate change.

This thesis has quantified the local nature of foraging within the fast ice environment, the influence of local environmental conditions on haulout and diving bout behaviour plus varied foraging strategies that all play a role in the sensitivity of Weddell seals to the changing environment. Using the nine criteria proposed by Laidre *et al.* (2008) and building on the work of Siniff *et al.* (2008) by incorporating these aspects of their winter ecology, we present an overview of the likely effects of global climate change on Weddell seals in Antarctica.

Sensitivity Criteria as they apply to Weddell seals

Under the scheme of Laidre, a species is awarded a criteria ranking between 1 (most sensitive to climate change) and 3 (least sensitive to climate change) in each of 9 variables. All sensitivity variables are considered to hold equal weighting, however it is likely that some variables may be more important than others especially on a species-specific basis. Nonetheless, the approach is a first step to gaining an understanding of the influence of climate change on marine mammals and allows assessment of the relative importance of each variable in the future as more information of predicted and actual changes in climate and the flow on effects to the environment are documented.

1) Population size

Species with larger populations have more options to adapt or re-establish in a new area after local extinctions (Laidre *et al.* 2008). The circumpolar population of Weddell seals has been estimated at 799,000 (Erickson and Hanson 1990) and 800,000 (Laws 1984). Most recently, the global population of Weddell seals was estimated by the APIS (Antarctic Pack-Ice Seals) program, initiated by the SCAR Group of Specialists on Seals and designed to address the known or potential biases of these earlier surveys of ice seals (Southwell *et al.* in review). Regional abundance for Weddell seals is highly uncertain and estimates are provided for just two Antarctic regions. In the 150°E to 100°W sector, Weddell seal numbers were estimated to be 331,000 (range of 144,000 – 759,000). For the 90°W to 30°W sector, the population was an estimated 302,000 (range of 77,000 – 576,000). In Laidre *et al.* (2008), the highest ranking, and correspondingly least sensitivity, to climate change regarding population size was allocated to species with a population > 500,000. Even though the regional population estimates derived by APIS are highly uncertain with a very large range (Southwell *et al.* in review), when coupled with previous estimates (Laws 1984; Erickson and Hanson

1990), it is highly likely that the global population is greater than 500,000. Accordingly, for this criteria Weddell seals can be assigned the highest ranking (3) indicating robustness to climate change.

2) Breadth/extent of geographic range

Species with a wide geographic distribution should be less vulnerable to climate change than species with narrow distributions given the regional differences in climate change in Antarctica (Laidre *et al.* 2008). For example, within the Antarctic Peninsula and Bellingshausen Sea, annual ice edge advance is now much later than it was and ice retreat is now much earlier along with the duration of the annual sea ice season becoming shorter (Stammerjohn *et al.* 2008). However, for the western Ross Sea, the opposite is occurring. Following Laidre *et al.* (2008), the Antarctic region was divided into eight 45° quadrants starting at 0° W. Ranking of sensitivity is assigned according to the number of quadrants occupied with the highest ranking (3) assigned to species that occupy all quadrants.

Weddell seals are regarded as having a circumpolar distribution (Lugg 1966; Kooyman 1981; Erickson and Hanson 1990). A review of current and historic Weddell seal scientific literature revealed that Weddell seals occur in each 45° quadrant. Literature regarding quadrant 0°W - 45°W locates Weddell seals along the Weddell Sea coast (Plötz 1986) and in particular around Drescher Inlet (Plotz *et al.* 2001). The 45°W – 90°W quadrant encompasses the populations of the Antarctic Peninsula (Bertram 1940; Casaux *et al.* 2006), South Georgia (Vaughan 1968), South Shetland Islands (Casaux *et al.* 1997) and the South Orkney Islands (Croxall and Hiby 1983). The 90°W – 135°W quadrant has no established Antarctic station which may account for the lack of Weddell seal literature associated with this area. However, approximately 250 Weddell seals occurring in groups of 10 – 20 around tidal cracks have been observed in

the vicinity of Siple Island (Lea and Soper 2005), which is located in this quadrant. A large volume of literature details Weddell seal populations in the 135°W – 180°W quadrant due to the presence of Scott (New Zealand) and McMurdo (United States of America) Antarctic bases (Dearborn 1965; Stirling 1969c; Testa 1994; Hadley *et al.* 2008). Weddell seal populations at the Japanese Antarctic base, Syowa, have been studied (Sato *et al.* 2003b) and occur in the 0°E – 45°E quadrant. In the 45°E – 90°E quadrant are the populations of the Mawson Coast and the Vestfold Hills (Lugg 1966; Rouget *et al.* 2007). Populations occurring near the retired Wilkes station occupy the 90°E – 135°E quadrant (Ingham 1960). For 135°E – 180°E quadrant, the populations of Commonwealth Bay and Adélie Land have been detailed (Sapin-Jaloustre 1952; Lake *et al.* 2003).

Weddell seals occurred in all 8 quadrants and as such, in terms of their range, the Weddell seal can be assigned the highest ranking (3) indicating robustness to climate change.

3) Habitat specificity

Habitat generalists can occupy a greater range of habitats than specialists and are therefore more buffered against the effects of climate change (Laidre *et al.* 2008). Laidre *et al.* (2008) present a list of Arctic habitats, the majority of which are also relevant as Antarctic habitats and include: shore-fast ice, loose annual pack ice, dense annual pack ice, multiyear pack ice, shear zones/leads, open water, shallow water/continental shelf, shelf break, deep ocean basins, estuaries/lagoons/fjords and land haulouts.

This study has shown that Weddell seals (at least the adult females) predominantly occupy the fast ice environment year-round. Other studies also highlight the importance of fast ice as a habitat for Weddell seals (Lake *et al.* 2005a; Lake *et al.*

2005b) with some suggesting that the pack ice zone may also be important (Smith 1965; Testa 1994), especially for young seals (Stewart *et al.* 2003). Shear zones/leads are important habitat features for Weddell seals as they allow access to haulout and breeding sites as well as access to air (Dearborn 1965; Siniff *et al.* 2008). This study has also shown that Weddell seals are constrained to foraging over the continental shelf and haulout locations include land. The Weddell seals in the Vestfold Hills region commonly occupied the fjords in that area (Lake *et al.* 2003) indicating that regionally, fjords have the potential to be important habitat features for Weddell seals. Polynyas also have the potential to be an important habitat feature for Weddell seals. One individual at the Vestfold Hills in 2006 was located within and on the border of a polynya in the Barrier Bay region for close to 4 months (this study). At Dumont d'Urville, Weddell seals have the opportunity to occupy polynyas due to a coastal polynya that occurs in relation to katabatic winds (Adolphs and Wendler 1995). Whilst open water is not often a feature of the winter habitat of Weddell seals, it is possible that the seals at Dumont d'Urville can access open water during winter due to ephemeral mid-season breakouts of fast ice (Massom *et al.* 2009). Once sea ice has retreated, Weddell seals can access open water. Weddell seals therefore have the potential to occupy at least ten different physical habitats which according to Laidre *et al.* (2008), allows them to be assigned the highest ranking (3) indicative of robustness to climate change.

4) Diet diversity

Species with a diverse diet should have decreased sensitivity to climate change (Laidre *et al.* 2008). In this study, we demonstrated that individual Weddell seals could be assigned a single dominant foraging strategy, benthic or pelagic. However, individual

seals also exhibited both strategies at some stage. This implies that the Weddell seals had the capacity to consume at least two different prey types – benthic and pelagic.

Diet specificity has been indicated in some studies, such as the dominance of *Pleuragramma antarcticum* in the diet of Weddell seals at McMurdo Sound (Burns *et al.* 1998). Recent research however suggests Antarctic toothfish *Dissostichus mawsoni* may be important prey for the McMurdo Sound population (Ainley and Siniff 2009). *Dissostichus mawsoni* are not often detected by diet studies as seals consume only the flesh, which does not appear in scat or stomach samples. Even so, Burns *et al.* (1998) conclude from stable isotope analyses that *Dissostichus mawsoni* did not contribute significantly to the seals' diet in McMurdo Sound.

Weddell seals are more commonly regarded as having generalist diets, for example taking benthic fish, pelagic fish and crustaceans in the Vestfold Hills (Green and Burton 1987; Green *et al.* 1995). In general, the primary prey reported for Weddell seals are fish followed by cephalopods and crustaceans (Southwell *et al.* in review). The varied foraging strategies encompassing benthic and pelagic behaviour (this study) also imply a generalist diet.

According to the criteria of Laidre *et al.* (2008) and assuming three or more species each comprise > 20% of the Weddell seal diet; Weddell seals are assigned the highest criteria ranking (3). At a regional level, this criteria ranking may not apply. For example, the population of Weddell seals at McMurdo Sound in which one prey species comprises > 20% of the diet makes this population more vulnerable to climate change.

5) Migrations

Migratory species may be more vulnerable to climate change due to temporal or seasonal reliance on a habitat (Laidre *et al.* 2008). Evidence suggests that large-scale movements of Weddell seals are rare. Different vocal patterns between populations

occur at distances greater than 600km (Abgrall *et al.* 2003) and the minimum distance required for genetic differentiation between populations is 700km (Davis *et al.* 2008). As reliance on sea ice as a physical structure is included as an additional variable (see below) and the findings of our study indicate that Weddell seals remain in the same general region throughout the year, according to the ranking criteria, Weddell seals should be assigned the highest ranking (3).

However, the migration criteria developed by Laidre *et al.* (2008) does not account for the impact of local movements. For example, in Chapter 4, the majority of Weddell seals occurring at Dumont d'Urville moved between Dumont d'Urville and Port Martin repeatedly throughout the winter. If such local movements are representative of the entire population at Dumont d'Urville, then local prey depletion may influence foraging success. At a finer scale, prey depletion is possible within the radius of a breathing hole or around an ice crack, especially if used by multiple seals (Kooyman 1975). Local prey depletion implies strong intraspecific competition which incidentally is linked to diversification of foraging strategies (Estes *et al.* 2003). It is possible therefore that a lack of migratory behaviour may make Weddell seals less robust to climate change as: i) the local habitat is under strong predatory pressure which may impact on foraging success, if seals are already experiencing resource limitations due to intraspecific competition, any changes to the local environment that reduce prey availability would also influence foraging success; and ii) Weddell seals rely solely on the local habitat as the winter ice environment constrains movement preventing the seals from leaving the local area to forage on more abundant prey elsewhere.

Relatively little is known about subadult movements however subadults in the Ross Sea appear to spend most of their time foraging in the pack ice (Stewart *et al.* 2003). There is high risk of predation by killer whales and leopard seals in the pack ice

environment with the potential to influence the subadult cohort (Stewart *et al.* 2003). If this behaviour is representative of the circumpolar population of subadult Weddell seals, then a significant proportion of the future breeding population is exposed to high predation risk due to occupation of the pack ice environment. This occupation can be considered as a migration from the fast ice environment to which subadults return when they are mature (Davis *et al.* 2008). Whist this isn't a migration linked to seasonal reliance on a habitat, it does indicate a reliance on the pack ice habitat to a cohort of the population. Climate induced change to the pack ice environment is likely to play a role in population demographics if it impacts the survival of subadults, lowering future recruitment into the breeding population.

Accordingly, we will consider Weddell seals to be vulnerable to change due to their complete reliance on the local habitat and the potential migration of subadults into the pack ice, with the lowest ranking assigned (1).

6) Individual site fidelity

Site fidelity is considered a component of sensitivity to climate change as heavy reliance on localities with predictable environmental conditions results in vulnerability to changes in those conditions (Laidre *et al.* 2008). Weddell seals exhibit high fidelity to spring haulout and breeding sites (Croxall and Hiby 1983) with the repercussions of site fidelity evident for the McMurdo Sound population (Siniff *et al.* 2008). In 2006, fast ice increased in thickness, extent and seasonal persistence due to the presence of an iceberg blocking the usual advection of sea ice from McMurdo Sound. Consequently, ice cracks that had been predictably present in previous years were closed off. This resulted in fewer adults arriving in the Sound with fewer pups born. It is not known if these females pupped elsewhere, however this event highlights the impact of reliance on

a particular location. As a result of this site fidelity, Weddell seals were assigned the lowest criteria ranking (1).

7) Influences of changes in sea ice

Sea ice as a physical structure is included as a component of sensitivity to climate change, taking into account a species reliance on sea ice to complete its life cycle or to feed (Laidre *et al.* 2008). Weddell seals rely on sea ice as a physical platform on which to haulout and pup. Already, the decline of a Weddell seal population at the Antarctic Peninsula has been linked to the reduction in area of sea ice necessary for breeding (Siniff *et al.* 2008). Adult females have also demonstrated higher age-specific probability of first reproduction at offshore colonies as opposed to inshore colonies in the Erebus Bay region indicating that the haulout site chosen for breeding plays a role vital rates (Hadley *et al.* 2008).

Weddell seals exhibit a diel haulout pattern (Andrews-Goff *et al.* 2010) hauling out on stable substrate adjacent to foraging grounds – often on fast ice (Lake *et al.* 2005b) and sometimes on land (this study). When diving, blood flow to the viscera is restricted (Davis *et al.* 1983). Therefore periods of quiescence during a dive, at the water surface, on land or on ice are required to digest prey (Crocker *et al.* 1997). Regular haulouts therefore may allow food processing, playing a similar role to that hypothesised for drift dives in elephant seals (Crocker *et al.* 1997). However, for the Weddell seal, food processing occurs while diving (Williams *et al.* 2004), has been documented while hauled out (Kooyman 1989) and for dives that do not exceed the aerobic dive limit, normal renal and splanchnic function is maintained (Davis *et al.* 1983).

Local environmental conditions play a role on the use of sea ice as haulout sites. In this study, we demonstrated that Weddell seals tend to haulout under conditions of

low wind speed and relatively higher temperatures and remain submerged when the wind is stronger and temperature colder, presumably as a thermoregulatory response. Climate predictions indicate that storm tracks will continue to shift pole-wards leading to increased winds and storms, especially over the summer and autumn (Turner *et al.* 2009). With increased storminess and winds, Weddell seals will spend less time hauled out on the ice. The implication of this is not clear but the possibility of decreased fitness exists if seals are forced to continue to expend energy remaining submerged and may be reluctant to remain hauled out throughout the breeding season impacting on reproductive success. Pup survival and condition have the potential to be influenced as Weddell seal pups may be forced to spend more time in the water before blubber is fully developed or remain on the ice alone with less opportunity to suckle.

A more serious problem is that fast ice haulout areas will become more vulnerable to break up or less stable (Massom and Stammerjohn 2010) resulting in loss of sea ice as a breeding and haulout platform. In addition, storms lead to periods of convergence in the sea ice motion field causing rapid and dynamic thickening of ice (Massom and Stammerjohn 2010) and presumably increasing the risk of ice cracks and leads closing over. This study has demonstrated the tendency for Weddell seals to terminate diving bouts under very heavy ice conditions in which the opportunity of locating a reliable ice crack or breathing hole may be limited. If Weddell seals avoid areas of very heavy ice, perhaps due to the risk of becoming trapped and increased storminess can close cracks and cause sudden increases in ice thickness, Weddell seal survival and foraging success can once again be linked to sea ice conditions. On the other hand, the advantage of remaining submerged under windy and cold conditions is that Weddell seals are able to protect themselves from the increasing winds and storms by remaining submerged throughout these periods.

Additionally, sea ice extent influences the population dynamics of Weddell seals in Erebus Bay with extensive winter sea ice linked to increased adult female survival (Hadley *et al.* 2006) and extensive summer sea ice linked to decreased foraging success (Proffitt *et al.* 2007). The link between sea ice extent and Weddell seal population dynamics is thought to be related to the relationship between sea ice and primary productivity (Hadley *et al.* 2007b). Extensive winter sea ice leads to a greater abundance of ice algae (Ross and Quetin 1991) that are released into the water column when the sea ice melts increasing marine productivity (Brierley and Thomas 2002). Extensive winter sea ice also increases the abundance of krill *Euphausia crystallorphias* (Loeb *et al.* 1997), which is a primary food source of *Pleuragramma antarcticum*, the principal prey of Weddell seals in this region (Dearborn 1965). If sea ice persists into summer however, the open water available for phytoplankton blooms is lacking which limits the primary productivity in the area with the flow on affect influencing Weddell seal foraging success (Hadley *et al.* 2007a). Sea ice predictions indicate that there will be a greater overall coverage of sea ice throughout the summer (Massom and Stammerjohn 2010) which will restrict access to spring breeding sites and lower foraging success.

Weddell seals therefore not only rely on sea ice as a physical platform for breeding (completing their life cycle) and resting (haulout) but also as an environment that mediates prey availability. As such, the lowest ranking criteria (1) is assigned when examining the relationship between influences of changes in sea ice on Weddell seals.

8) Influence of changes in the trophic web

Changes in primary and secondary production due to climate change (Laidre *et al.* 2008) may result in new or alternate species within the local foraging environment or

the disappearance of current prey species. This is a subjective classification based on knowledge of food chain relationships and projected changes due to climate change.

In general, fish, primarily *Pleuragramma antarcticum*, are the dominant prey taken by Weddell seals throughout their range (*i.e.* Burns *et al.* (1998), Lake *et al.* (2003), Plötz *et al.* (1986), Casaux *et al.* (2006), Testa (1994)). The life cycle of *Pleuragramma antarcticum* is tightly linked to the Antarctic sea ice that is a key habitat throughout the life cycle and operating as a food source via its influence on the abundance of *Euphausia crystallorphias.*

Pleuragramma antarcticum use the underside of ice as a nursery for eggs and for foraging of newly hatched larvae (Vacchi *et al.* 2004). Survivorship of larvae therefore should be enhanced when sea ice is extensive (Moline *et al.* 2008). Larval and juvenile *Pleuragramma antarcticum* feed primarily on copepods (Hubold 1985) whilst adults consume *Euphausia superba* or *crystallorphias* (De Witt and Hopkins 1977). Given the positive relationship between sea ice extent and krill abundance, extensive winter sea ice will result in increased foraging capacity and consequently survival for *Pleuragramma antarcticum. Euphausia superba* abundance has declined with declining sea ice (Atkinson *et al.* 2004) and a substantial loss of sea ice is projected over the 21st century (IPCC 2007). The availability of *Euphausia crystallorphias* to higher predators is also linked to the ice environment (Ainley *et al.* 1998). Unfortunately, *Pleuragramma antarcticum* has low recovery potential due to limited emigration, slow growth and low fecundity making it the "Achilles heel" of the Antarctic food web (Mintenbeck 2008). Occupying a similar role to that played by sardines and anchovy in upwelling systems, any systemic shift that affects *Pleuragramma antarcticum* will alter the trophic web considerably. The potential exists for severe consequences to top predators and ecosystem functioning in general.

In most regions, *Pleuragramma antarcticum* shares pelagic waters with the Antarctic toothfish, *Dissostichus mawsoni* (Moline *et al.* 2008), potentially an important prey species of Weddell seals (Ponganis and Stockard 2007; Ainley and Siniff 2009). Ainley & Siniff (2009) recommend that a fishery in the Ross Sea targeting *Dissostichus mawsoni* be reduced or risk causing dramatic changes to the local Weddell seal population.

This study has indicated that Weddell seals have plastic foraging strategies with the ability to switch between benthic and pelagic foraging. It is also likely that consumption of multiple prey species is the norm (Lake *et al.* 2003). However, given the reliance of Weddell seals on *Pleuragramma antarcticum* throughout their range and the reliance of *Pleuragramma antarcticum* on *Euphausia crystallorphias*, changes to the abundance of this species would impact Weddell seal populations. The extent of this impact will be governed somewhat by the availability of alternate prey species. With the ability to switch between pelagic and benthic foraging, and with cephalopods and crustaceans occurring secondary to fish in the diet of Weddell seals (Southwell *et al.* in review) it is likely that the carrying capacity of Weddell seals will not be affected by changes to the trophic web. Accordingly, we will assign the mid range criteria ranking to Weddell seals (2) indicating moderate vulnerability to climate change.

9) Maximum rate of population increase (R_{max})

Species with high growth potential are more capable of exploiting optimal environmental conditions as they arise whilst species with low growth rate are slow to recover from deleterious changes in population (Laidre *et al.* 2008). In the absence of stock-specific measured values, approximate values can be used for R_{max} near the lower range of measured or theoretical values (Wade and Angliss 1996). Following Wade & Angliss (1996), Laidre *et al.* (2008) assumed a maximum theoretical net productivity

rate for phocids of 12%. Assuming 12% is the theoretical minimum of the maximum rate of population (Wade & Angliss 1996) and the potential for the maximum rate of increase for Weddell seals to be as high as 20% (Schmitz and Lavigne 1984), we assign the highest criteria ranking (3). According to the criteria developed by Laidre *et al.* (2008), species with a maximum rate of population increase > 10% are assigned this highest ranking indicating robustness to climate change.

Sensitivity index for Weddell seals and Arctic marine mammals

Out of a maximum possible score of 27 indicating least sensitivity across all variables, and a minimum possible score of 9 indicating most sensitivity across all variables, Weddell seals were assigned a score of 20. When relating this score to the sensitivity index derived by Laidre *et al.* (2008) for Arctic marine mammals, Weddell seals are slightly less sensitive to climate change than the Subarctic pinnipeds but more sensitive than the Arctic pinnipeds (Table 5.1).

According to Laidre *et al.* (2008), species that scored between 16 and 20, such as Weddell seals, were classified as moderately sensitive to climate change. The least sensitive of the Arctic species were the Weddell seals' northern counterparts, the ice-associated pinnipeds, bearded and ringed seals, scoring 23 and 25 respectively. Weddell seals sit on the cusp between the "moderately sensitive" and "least sensitive" classification and exhibit most of the properties common to the "least sensitive" species, which include a circumpolar distribution, large population size, a varied diet and flexible habitat requirements. Highly sensitive species were more restricted in distribution, less abundant or habitat specialists.

Table 5.1: Sensitivity index for the Weddell seal and Arctic marine mammals. Arctic marine mammal sensitivity was derived and extracted from Laidre *et al.* (2008) whilst the sensitivity for Weddell seals was determined in this study. Weddell seals are regarded as moderately sensitive to climate change making them slightly more sensitive than their Arctic pinniped counterparts, the ringed and bearded seals that are regarded as the least sensitive of the Arctic marine mammals.

Species	Population size	Geographic distribution	Habitat specificity	Diet diversity	Migration	Site fidelity	Sea ice changes	Trophic web changes	R_{max}	Total
Antarctic										
Weddell seal	3	3	3	3	1	1	1	2	3	20
Arctic										
Beluga	2	2	2	2	2	1	3	3	1	18
Narwhal	1	1	1	1	1	1	3	2	1	12
Bowhead whale	1	2	2	2	1	2	3	2	1	16
Ringed seal	3	3	3	3	3	3	1	3	3	25
Bearded seal	2	3	2	3	3	3	1	3	3	23
Walrus	2	2	2	2	2	2	1	3	2	18
Polar bear	1	3	2	1	2	2	1	1	1	14
Subarctic										
Spotted seal	2	1	3	3	2	2	1	2	2	19
Ribbon seal	2	1	3	2	2	3	1	2	3	19
Harp seal	3	1	3	3	1	1	1	3	3	19
Hooded seal	2	1	2	2	1	1	1	2	3	15

Ringed seals have been likened to Weddell seals (Stirling 1969b; Smith *et al.* 1991; Wartzok and Davis 1992) due to their ability to inhabit the fast ice year round, maintaining breathing holes with the claws on their fore flippers (Vibe 1950). The species differ significantly in other regards. The ringed seal is comparatively smaller and is preyed upon by polar bears and arctic foxes, as opposed to the Weddell seal that experiences minimal predation pressure (Smith *et al.* 1991). This predation pressurecombined with cold exposure has lead to ringed seals taking shelter in subnivean lairs.

Bearded seals, on the other hand, are of comparatively similar body size to Weddell seals. However, they are usually associated with the pack ice environment and shore leads (Burns 1970) and only occasionally occur in shore-fast ice (Stirling and Smith 1977). Like Weddell seals, the winter ice conditions restrict bearded seals from moving away from their over wintering sites and bearded seals sometimes maintain breathing holes in the ice (Davis *et al.* 2008).

Weddell seals, bearded seals and ringed seals differ significantly in only one sensitivity variable (excluding the migration variable due to our modification of the criteria). Weddell seals were ranked as highly sensitive (1) in relation to site fidelity as opposed to both the ringed and bearded seals ranking least sensitive (3). Interestingly, like Weddell seals, bearded seals have significant geographical variation in vocal repertoire (Cleator *et al.* 1989) and a high degree of population structure (Davis *et al.* 2008). This indicates the potential for bearded seals to exhibit strong site fidelity however this has not yet been demonstrated.

Weddell seals, bearded seals and ringed seals are all highly sensitive to changes in sea ice. Not surprisingly, high sensitivity to changes in sea ice was assigned to all Arctic and Subarctic pinnipeds in addition to polar bears (Laidre *et al.* 2008). For all

these species, this high sensitivity is driven by a decrease in ice extent and stability. Sea ice extent directly impacts polar bears that use the sea ice to access denning areas and as a hunting platform, and influences the extent to which walruses can exploit feeding areas. Stable pack ice is critical for ice-breeding phocids until pups are weaned. For the ice associated Weddell, bearded and ringed seals, changes in sea ice will result in habitat suitable for breeding being inaccessible, reduced in size or lost completely.

Overall, Weddell seals are moderately sensitive to climate change and their future in the face of a changing climate and particularly, changes in sea ice is not bleak. This study has demonstrated the flexible foraging nature of these seals and is optimistic about their ability to switch prey if the need arises. This study has also highlighted their ability to avoid cold and windy weather by remaining submerged and indicates that the prediction of increased storm and wind is not likely to impact their survival. The biggest threat to Weddell seals are the predicted changes in sea ice that may remove suitable habitat for pupping and reduce prey availability.

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